ECOLOGICAL STUDIES OF THE PSOCID *LIPOSCELIS* *RUFA* BROADHEAD (PSOCOPTERA: LIPOSCELIDIDAE)

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ECOLOGICAL STUDIES OF THE PSOCID *LIPOSCELIS*

RUFA BROADHEAD

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CHAPTER I

INTRODUCTION

Psocoptera (psocids) is a relatively small order of insects with about 5,500 species worldwide. In the last two decades, psocids have risen to prominence because species in the genus *Liposcelis* (Liposcelididae) have become serious stored product pests in many parts of the world (Kalinovic et al. 2006, Kučerová 2006, Nayak 2006, Throne et al. 2006, Rees 2008, Ahmedani et al. 2010, Phillips and Throne 2010). Traditionally, psocids have been considered scavengers that fed on molds and were thought to be of negligible importance as pests. Psocids were overlooked because of their small size and due to the presence of more serious coleopteran and lepidopteran stored product pests that influence pest management strategies in stored commodities. However, over the last 20 years they have emerged as serious pests of stored commodities worldwide and recent studies have shown that the status of psocids has changed from nuisance pests to worldwide pests of stored products (Turner 1999, Kučerová 2002, Pascual-Vil-Lalobos et al. 2005, Throne et al. 2006, Opit and Throne 2008, Gautam et al. 2010). For example, prior to the 1990's in Australia and China and before the 2000's in the United States, psocids were not considered pests of serious economic importance (Nayak 2006, Phillips ad Throne 2010).

Most of the psocid species that are pests of stored product commodities are in the family Liposcelididae and belong to genus *Liposcelis*. These have been reported as serious pests of stored product in several countries around the world including the United States (Lienhard and Smithers 2002, Mockford and Krushelnycky 2008), United Kingdom (Turner 1994), Spain (Pascual-Villalobos et al. 2005), Australia (Rees 1998, 2003, 2008), Mexico (Garcia-Aldrete and Gutierrez Diaz 1995), Portugal (Kučerová 2006), Zimbabwe (Mashaya 2001), and Asian countries like India, Indonesia, China, Malaysia, Singapore, Philippines, and Thailand (Rajendran 1994, Kleih and Pike 1995, Leong and Ho 1995, Wang et al. 1999a, Chin et al. 2010). Psocid species known to infest stored grain in North America (Mockford 1993, Lienhard and Smithers 2002) are; *Liposcelis bostrychophila* Badonnel (Psocoptera: Liposcelididae), *Liposcelis decolor* (Pearman), *Liposcelis entomophila* (Enderlein), *Liposcelis paeta* Pearman, *Liposcelis brunnea* Motschulsky, *Liposcelis corrodens* (Heymons), and *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae). The former four *Liposcelis* species are reported to be a serious problem in Australia (Rees 2008). In addition, *Liposcelis rufa* Broadhead has been found infesting stored wheat in Stillwater, OK, USA (Gautam et al. 2010).

The rise in the pest status of psocids can be attributed to: 1) their varying response to physical and chemical management tactics that are effectively used to control coleopteran pests of stored products, e.g., some psocid species are resistant to residual insecticides and the fumigant phosphine (Nayak et al. 2002a); 2) repeated failure of usual practices of protection and disinfection to control psocids (Wang et al. 1999a, Beckett and Morton 2003, Nayak et al. 2003a, 2003b; Nayak and Daglish 2007); 3) the quantitative loss they cause by feeding on the endosperm and germ (Kučerová 2002); and

4) their ability to deteriorate the quality of stored commodities by the presence of live and dead insects, fecal material, and exuviae and distribution of moulds (Obr 1978, Chin et al. 2010). In addition, the rising consumer concern about quality produce may lead to rejection of commodities destined for export that are infested with psocids; thereby causing economic losses. In countries such as Australia, psocid infested grain is banned for export (Nayak 2006, Nayak 2010). Furthermore, psocids are reported to be associated with health problems because they cause allergic reactions in sensitized people.

As previously mentioned, *L. rufa* has been found infesting stored commodities in large numbers in Portugal, Australia, and the United States (Kučerová 2006, Rees 2008, Gautam et al. 2010). Faunistic records show that *L. rufa* was first reported in the United States from Hawaii in 1985 (Mockford and Krushelnycky 2008), yet published studies are lacking for this species. Detailed biological studies have been done on *L. reticulatus* (Opit and Throne 2008, Opit et al. 2010a), *Liposcelis badia* Wang, Wang and Lienhard (Jiang et al. 2008), *L. bostrychophila* (Rees and Walker 1990, Turner 1994, Wang et al 2000), *L. brunnea* (Opit and Throne 2009), *L. decolor* (Tang et al. 2008), *L. entomophila* (Rees and Walker 1990, Leong and Ho 1995, Wang et al. 1998), *L. paeta* (Rees and Walker 1990, Wang et al. 2009), and *Liposcelis tricolor* Badonnel (Dong et al. 2007). However, there is a dearth of published information on the biology of *L. rufa and L corrodens*. Increased understanding of the ecology and biology *L. rufa* is crucial for the development of management strategies against this pest. Therefore, in order to develop effective management strategies for *L. rufa*, I initiated experiments to elucidate the effects of environmental conditions on its biology and ecology.

Objectives

Psocids have emerged as serious pests of stored commodities in the United States during the last decade. Prior to 2000, there was little published information on the biology and the ecology of psocids (Opit et al. 2010b). However, the recognition of psocids as pests of stored grain and grain processing facilities in the United States (Phillips and Throne, 2010) and the limited amount of published information on their biology prior to the 2000s led USDA-ARS Center for Grain and Animal Health Research (CGAHR), Manhattan, KS, USA to launch ecological studies of psocids infesting stored commodities in the United States in 2004 (Opit et al. 2010b). The only other place that conducts psocid research in the United States is the Stored-Product Entomology Laboratory at Oklahoma State University, Stillwater, OK, USA (Opit et al. 2010b).

The general lack of information on psocid ecology is partly due to their recent emergence as stored grain pests and their small size. In addition, their taxonomic complexity makes them difficult to identify (Mockford 1971). Furthermore, techniques to perform biological studies that existed prior to 2004 were not user friendly (Opit et al. 2010b). New techniques have since been developed (Opit and Throne 2008). As a result, detailed biological studies have been conducted on several pest species of psocids (see above). However, there is no published information available on the ecology and biology of *L. rufa* which has been reported as a pest of stored wheat in Oklahoma (Gautam et al. 2010). Given this lack of information, I initiated experiments to elucidate the influence of temperature and relative humidity on the population growth of *L. rufa* and the effects of temperature on its development and reproductive parameters.

The objectives of my thesis are:

Objective 1:

Determine the effects of constant temperatures and relative humidities on the population growth of *L. rufa*.

Objective 2:

Determine the effects of constant temperatures on the development of *L. rufa*.

Objective 3:

Determine the effects of constant temperatures on the reproductive parameters of *L. rufa*.

CHAPTER II

LITERATURE REVIEW

Psocoptera

Fossil records indicate that, psocids first originated in the Permian era, about 295-248 million years ago (Christopher 2002). Phylogenetically, psocids (Psocoptera) are related to lice (Phthiraptera), thrips (Thysanoptera), and aphids (Hemiptera) (Lyal 1985). All these orders belong to the super order Paraneoptera, reflecting diverse feeding habits. Among insects in this group, psocids are considered as the most primitive hemipteroids (Lyal 1985). Their name, psocoptera is derived from the Greek word, *psokos* which means gnawed or rubbed, and *ptera,* which means wings (Ahemdani et al. 2010). Psocids are small (1-6 mm), fast running insects with large heads, prominent black eyes, long antennae, and small thoraces. Body color varies with species, but many are pale yellow with brown abdominal bands (Mockford 1971). They are commonly known as book lice or bark lice, which describes their habitat among old and moldy books, where they feed on fungus growing on the paper and starchy glue used for binding. Despite their common name, which associates them with human head and body lice, psocids are not parasitic in nature. There are more than 5,500 species of psocids from 3 suborders and 41 families distributed all over the world (Ahmedani et al. 2010). Most psocid species are found

outdoors and have well developed wings. They live under the bark of trees and among dead leaves and feed on molds, and are therefore, of little importance as pests. Other psocid species are found indoors, preferring to live in closed building structures. These species, especially *Liposcelis* spp., create problems in domestic conditions (Baz and Monserrat 1999), in grain storage areas (Turner 1994, Rees 2003, Throne et al. 2006), and in museums where they feed on dead specimens (Chin et al. 2010). Although, indoor species of psocids are suspected to feed on molds and fungus, they have been observed feeding on the endosperm and germ of grain kernels (Kučerová 1999, 2002), which have no fungal contamination. Psocids can potentially cause distinct problems for e.g. qualitative degradation of the stored commodities by contamination with live and dead specimen (Obr 1978) and through the transfer of microorganisms (Kalinovic et al. 2006, Beher et al. 2010) and quantitative losses by feeding (Kučerová 1999, 2002) in areas of food and grain storage, and are especially prevalent in hot and humid areas (Wang et al. 1998). However, the psocid pest problem is not confined to tropical areas but exists in temperate regions as well (Opit and Throne 2008).

Worldwide Distribution of Psocids

Psocids are believed to be native to tropical and sub tropical regions of the world, for example Africa. However, reports indicate that they have a cosmopolitan distribution and are continually disseminated throughout the world by means of trade (Kučerová 2006, Rees 2008, Ahemdani et al. 2010). According to Schneider (2010), of the 231 species of psocids found in Europe, 49 are of alien origin adapted to live in indoor habitats where they cause distinct problems as pests. Psocids have cosmopolitan distribution. Infestations of psocids have been reported in stored grains from the United

States (Throne et al. 2006, Gautam et al. 2010), United Kingdom (Turner 1994), Australia (Rees and Walker 2000, Nayak 2006, Rees 2008), Europe (Schneider 2010), China (Wang et al. 1999a, 1999b; Jiang et al. 2008), Czech Republic and Portugal (Kučerová 2006), India and Indonesia (Kleih and Pike 1995), Zimbabwe (Mashaya 2001), and Croatia (Kalinovic et al. 2006). Psocid species that have been found infesting stored grain in the United States are: *L. reticulatus, L. bostrychophila, L. decolor, L. entomophila, L. paeta, L. brunnea, and L. corrodens* (Mockford 1993, Lienhard and Smithers 2002). In addition, *L. rufa* has been found infesting stored wheat in Oklahoma (Gautam et al. 2010). According to Ahemdani et al. (2010), besides the eight species of psocids already listed, seven other species infest stored commodities in the United States which includes: *Lepinotus inquilinus* Heyden (Trogiidae), *Lepinotus patruelis* Pearman, *Trogium pulsatorium* Linnaeus (Trogiidae), *Lachesilla pedicularia* Linnaeus (Psocoptera: Lachesillidae), *Liposcelis divinatorius* Muller, *Liposcelis mendax* Pearman, *Liposcelis terricolis* Badonnel. According to Rees (2008), eleven species of psocids, eight of which are *Liposcelis* spp., are reported as of grain storage in Australia. In addition, seventeen species of psocids are reported from Croatia, where *L. decolor* is the most encountered species along with nine species from the family Liposcelididae (Kalinovic et al. 2006).

Psocids as pests in stored grains

The small size of stored grain psocids (≈ 1 mm), the manner in which they feed on grain, and the presence of more damaging stored product pest have limited their perceived importance as pests (Nayak 2006, Jiang et al. 2008). Several reports published during the 1990s and the 2000s have elucidated their status as an additional threat to global food security (Nayak 2006, Throne et al. 2006, Rees 2008, Phillips and Throne

2010). *L. entomophila* and *L. decolor* are the predominant species infesting stored wheat in the United States (Throne et al. 2006, Opit et al. 2009a). On the other hand, *L. bostrychophila* along with *L. decolor* are the predominant species infesting stored barley, wheat, and lupins in Australia followed by *L. entomophila*, and *L. paeta* (Rees 2008). In Portugal, *L. decolor* and *L. entomophila* are the most encountered species on stored rice, followed by *L. tricolor*, *L. rufa*, and *L. bostrychophila* (Kučerová 2006). In other countries such as Britain, Denmark, and the Netherlands, *L. bostrychophila* is a major pest in households (Turner 1986). Seasonal fluctuations of temperature and relative humidity may be key factors determining the species composition in storage areas (Mashaya 2001, Opit et al. 2009b). Psocid infestations usually involve a couple of species or multiple species of *Liposcelis* and/ or *Lepinotus* spp.; however, there are cases of only single species infestation (Opit et al. 2009b). It is likely there are other psocid species infesting stored grain that have not been documented. This observation is supported by the fact that *L. rufa*, which was previously not considered a pest (Mockford and Krushelnycky 2008), was recently found infesting stored wheat in Oklahoma (Gautam et al. 2010). However, before this, it had also been found in stored rice in Portugal (Kučerová 2006) and in imported wood in Australia (Rees 2008). It is very likely that *L. rufa* has been infesting stored commodities for a long time before these preceding recent reports.

Economic importance of Psocids

The rise of psocids to prominence

Despite the fact that psocids have been associated with stored commodities for a long time, they were regarded as secondary pests of low economic importance until the 1990's in Australia and China and the 2000's in the United States (Phillips and Throne 2010). At present, psocids are one of the most frequently encountered stored product pests in certain parts of some countries such as Australia (Rees 2003). Differential response of psocid species to the most commonly used chemicals for the control of stored product pests is a possible key contributing factor to their rise to prominence. For example, several species of psocids have developed resistance to phosphine; the most commonly used stored grain fumigant (Nayak et al. 2003a, 2003b). Physiological and behavioral peculiarities have provided psocids with tools to fight chemical treatments, for example, their ability to delay egg hatch in phosphine-rich environments and the ease with which they move out of storage structures that are under fumigation allows them to avoid exposure to grain protectants (Nayak et al. 2003a, Phillips and Throne 2010). Another factor thought to contribute to the increasing prominence of psocids is the fact that most pesticides used for the control of stored product pests are effective against coleopteran pests, which predate on psocids, but are not effective against psocids. This frees the psocids from predation and competition thereby contributing to population explosions (CSIRO 2004). The fact that commodities infested by psocids can be rejected for export (Kučerová 2002, Nayak 2006, 2010) has also contributed to their increased prominence. There are other attributes of psocids that make them serious pests. For example, some species are parthenogenetic, with an ability to survive for long periods

without food (Turner and Maude-Roxby 1988), and the high reproductive capacity (Opit et al. 2010a) facilitates colonization and establishment in new habitats.

Quantitative losses caused by psocids

Psocids are documented as being predominant in moist and damp habitats, which are favorable for fungal growth (Mashaya 2001). However, recent literature suggests that psocids can thrive in less than damp and moist environments (Opit et al. 2009a, 2009b; Gautam et al. 2010, Opit et al. 2010b). According to Kučerová (1999), psocids feed and thrive on germ and endosperm which do not have any fungal contamination. Psocids appear to have a preference for germ but will also feed on the soft endosperm of damaged or cracked kernels (Kučerová 1999). As a result of harvesting and handling operations, stored grain has plenty of damaged kernels which provide an ideal environment for the psocids to multiply (Rees 2008); in fact, cracked (damaged) wheat has been demonstrated to increase progeny production (Athanassiou et al. 2010a). Large populations of psocids, typical of those found in grain storages during certain times of the year, have been reported to cause considerable weight loss in grain by feeding on the endosperm and germ (Kučerová 2002). McFarlane (1982) recorded weight losses of up to 4-5% caused by *L. bostrychophila* feeding on rice after 6 months of storage. Pike (1994) also reported 2.9% weight loss in lightly milled rice after 3.5 months of *L. paeta* infestation. A study by Kučerová (2002) showed that *L. bostrychophila* causes weight losses of up to 9.7% in cracked wheat kernels after 3 months infestation. Besides negatively impacting quantitative aspects of grain, psocids also cause qualitative loss. Psocid infested products are of low economic value, due to contamination by live and dead specimens, cast skin, and feces (Kučerová 2002), and by the presence of microorganism (Obr 1978).

Health concerns and safety hazards associated with psocids

Psocids can multiply rapidly resulting in large populations under favorable environmental conditions (Opit and Throne 2008, 2009, Gautam et al. 2010, Opit et al. 2010b). Psocid numbers in grain storages can become so large that they appear like brown carpets on surfaces. Populations this large cause discomfort among store-house workers by crawling on them. They are also a safety hazard because they create slippery condition on floors used by workers. Psocids are documented to cause health problems in humans. Turner and Ali (1996) demonstrated that at least 5% of allergy patients exhibited strong positive reactions to the *L. bostrychophila* antigen. Psocids may not be responsible for allergies only, Beher et al. (2010), demonstrated that *L. bostrychophila* is capable of harboring and transmitting *Rickettsia felis,* bacteria that causes typhus-like fever in humans. Psocids may also affect human health by being "ectoparasites". Lin et al. (2004) trapped *L. bostrychophila* abandoning patient's nail infected with onychomycosis, fungal infection of nail which causes nail hardening (Rehmus 2009). Psocids have also been reported to act as intermediate hosts by consuming tapeworm eggs, harboring the larvae inside their gut, and disseminating the parasites in their environment (Turner 1994). In some studies, psocids that fed on disease causing fungi were found capable of disseminating these pathogens (Kalinovic et al. 2006). Much more extensive research on psocid-associated health problems needs to be conducted to confirm their role as a vector of human and animal diseases.

Management of psocids

Compared to the major stored-product beetle pests, little research has been conducted on the ecology and biology of stored-product psocids. In addition, many of the studies conducted on stored-product psocids have focused on their management with a few studies on their ecology and biology. Moreover, management studies have been particularly focused on *L. bostrychophila, L. decolor, L. entomophila,* and *L. paeta,* which are reported to be the most encountered species in stored commodities in country such as Australia (Rees 2008). Phosphine, which is a widely used fumigant for the control stored-product pests, has been demonstrated to effectively control psocids if applied to grain in a fully sealed system (Nayak et al. 1998, CSIRO-SGRL 2003). However, efficiency is reduced because many systems are leaky. According to Nayak et al. (2002a, 2002b), resistance to phosphine builds rapidly and high levels of resistance to phosphine have been detected in psocids infesting stored commodities in Australia. In many cases, phosphine has failed to control psocids (Rees 1998).

Organophosphates such as fenitrothion and diazinon are highly effective (Turner 1988), however carbamates and pyrethroid insecticides are not (Turner 1994). Athanassiou et al. (2010) demonstrated approximately 100% mortality when a combination of chlorpyriphos-methyl and deltamethrin was used against *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta*. According to Nayak (2010), synergized pyrethrin (Piperonyl butoxide) provided up to 3 months protections for these species of psocid on treated grain (6 $mgkg^{-1}$). Carbamates in combinations with organophosphate insecticides (azamethiphos, chlorpyrifos-methyl, or pirimiphos-methyl) applied as structural treatments are reported to provide long-term protection of up to 40

weeks (Nayak et al. 2003b), whereas carbamate with fenitrothion gives a shorter protection of up to 8 weeks against *L. bostrychophila, L. entomophila,* and *L. paeta*. Nicotinoids such as imidacloprid are effective against *L. bostrychophila*, *L. decolor*, *L. entomophila*, and *L. paeta* (Nayak and Daglish 2007), but the high application rate of 10 mg kg^{-1} required makes it more suitable as a seed treatment rather than a grain protectant.

Spinosad is a newly developed bacterium-derived protectant that can be effectively used to manage *Rhyzopertha dominica* and *Cryptolestes ferrugineus* (Subramanyam et al. 2007). However, spinosad has been shown to be ineffective against *L. bostrychophila*, *L. decolor*, *L. entomophila,* and *L. paeta* on wheat (Nayak and Daglish 2007). A combined treatment of 1 mg kg^{-1} spinosad plus 10 mg kg^{-1} chlorpyrifos-methyl can control all the four *Liposcelis* species, but the high application rate of 10 mg kg^{-1} of chlorpyrifos methyl may restrict its use to seed treatments only (Nayak and Daglish 2007). The insect growth regulator fenoxycarb effectively reduced progeny production of *L bostrychophila* at low doses and seems to be effective against psocids (Buchi 1994). According to Wei et al. (2002), controlled atmosphere (35% CO_2 and 1% O_2) and organophosphate insecticides (e.g. dichlorvos) slows the development of resistance by psocids to both tactics, and also provides a significant increase in mortality compared with using these procedure individually. However, according to Wang et al. (1999a) psocids are capable of developing resistance to controlled atmosphere.

Psocids are external feeding stored product pests which can be effectively controlled using cultural management practices. Good sanitation, such as empty bin clean-up and disinfestations using fumigants or residual pesticides could ensure that psocid numbers are at extremely low levels when storages are filled with grain or other

commodities. Removal of grain debris eliminates an ideal environment for the development of early populations and may play a key role in the management of psocids (Rees 2008). Psocids flourish in environments where relative humidities are high (> 63% RH) but do not survive below 55% RH (Opit and Throne 2008, Opit and Throne 2009, Gautam et al. 2010). Physical control through, for example, lowering of relative humidity slows the population growth, development, and multiplication of psocids (Opit and Throne 2008, Opit and Throne 2009, Gautam et al. 2010). Reduction of relative humidity levels in grain storages can be achieved through storage of low moisture content grain and ensuring there are no water leaks.

Beckett and Morton (2003) have demonstrated that psocids are considerably more vulnerable to heat disinfestation at moderately elevated temperatures (45-55^{o}C) than other stored product insect pests, for example *R. dominica* and *S. oryzae*. Therefore, heat disinfestation appears to hold some promise for the control of psocids. This could especially be used in the disinfestation of empty storage structures before they are filled with grain or other commodities.

Psocid ecological studies

A few detailed studies have been conducted on the biology of psocids (Fahy 1971, Khalafalla 1990, Wang et al. 1999b, Wang et al. 2000; Wang et al. 2001). Moreover, many of these studies have been conducted outside North America and have focused on *L. bostrychophila*. These three preceding facts and the recognition of psocids as pests of stored grain and grain processing facilities in the United States (Phillips and Throne 2010) led the USDA-ARS Center for Grain and Animal Health Research (CGAHR), Manhattan, KS, USA initiate ecological studies of psocids infesting stored commodities

in the United States in 2004. The Stored-Product Entomology Laboratory at Oklahoma State University, Stillwater, OK, USA has since joined CGAHR in conducting psocid research in the United States.

The fact that psocids were considered mere nuisance pests until the 1990s was probably partly responsible for the limited amount of published information available on their biology. The small size of psocids (≈1 mm) and the difficulty handling and identifying them could also be other contributing factors. Furthermore, the techniques used to conduct biological studies on psocids prior to 2004 were laborious, imprecise, and not user friendly. The aforementioned studies (Fahy 1971, Khalafalla 1990, Wang et al. 1999b, Wang et al. 2000, Wang et al. 2001) mostly investigated the effects on physical conditions on the development and population dynamics of psocids. These studies showed that psocids do not survive at relative humidities (RH) below 60% and thrive at temperatures of 30 to 33°C. Other studies have also found the optimal temperature for development of the *Liposcelis* spp. to be between 30 and 35°C, at which is development completed in 21 to 30 days (Opit and Throne 2008, 2009; Gautam et al. 2010, Opit unpublished data).

In recent years several studies have been conducted on the biology of stored product psocids, and the species investigated were *L. brunnea*, *L. rufa*, *L. pearmani*, and *L. reticulatus* (Opit and Throne 2008, 2009; Gautam et al. 2010, Opit et al. 2010a, 2010b). Specifically, these studies have investigated the effects of temperature and relative humidity on population growth, developmental, and reproductive parameters of these four species.

Effects of Temperature and Relative Humidity on Population Growth.

L. brunnea, *L. rufa*, *L. pearmani*, and *L. reticulatus* will not survive at 43% RH. At 55% RH, *L. reticulatus* will not survive; *L. rufa* and *L. pearmani* will survive between 22.5 and 30°C; and *L. brunnea* between 22.5 and 35°C. At 63% and 75% RH, *L. pearmani* and *L. brunnea* will not survive above 35°C. *L. rufa* will not survive at 40°C and 63% RH but will survive at 40°C and 75% RH (Opit and Throne 2008, 2009; Gautam et al. 2010, Opit et al. 2010b). Of these four species, *L. reticulatus* appears to survive under the narrowest set of conditions and appears suited to cooler and more humid conditions. *L. brunnea* and *L. pearmani* appear capable of surviving under a much wider range of conditions ranging from 22.5 to 35°C and 55% to 75% RH (Opit and Throne 2009, Opit et al. 2010b). The ability of *L. rufa* to multiply at 55% RH, at temperatures of 22.5, 25, 27.5, and 30.0°C may allow it to thrive under conditions of low relative humidity where other *Liposcelis* species may not. In addition, its ability to multiply rapidly at high temperatures of 35 and 37.5°C and 75% RH may allow it to thrive at temperatures too high for most *Liposcelis* species. Therefore, *L. rufa* appears to have the widest distribution of these four species (Gautam et al 2010). Optimal breeding conditions for *L. brunnea*, *L. rufa*, *L. pearmani*, and *L. reticulatus* were 32.5°C and 63% RH; 35°C and 75% RH; 32.5°C and 75% RH; and 30 and 32.5°C and 75% RH, respectively. Starting from an initial population of five females each, populations of these psocid species grew by 17-, 73-, 31-, and 21-fold, respectively, under optimal conditions (*L. reticulatus* populations increased over a 46-d period whereas those of the other three species was over a 30-d period). Among these species, *L. rufa* populations grew fastest. Another fact to note here is *L. reticulatus* is parthenogenetic species while others are not.

Based on the studies cited, the predicted size of the range of the four species in declining order would be: *L. rufa*, *L. brunnea* and *L. pearmani*, and *L. reticulatus*.

Effects of Temperature on Development.

Temperatures have been shown to have no effect on egg viability of *L. rufa*, *L. brunnea*, and *L. reticulatus*. Average percentages of viable eggs across all temperatures that were tested (22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, and 40.0°C) were 90, 87, and 80%, respectively. Nymphal survivorship averaged 78, 63, and 36%, respectively. The low nymphal survivorship for *L. brunnea* and *L. reticulatus* may be due to the susceptibility of nymphs to handling or that the relative humidity in which the development studies were conducted (75%) was not the optimal RH for these species. The fact that *L. brunnea* populations were higher at 63% RH than at 75% RH appears to support this explanation (Opit and Throne 2009). The shortest development times for the egg and combined nymphal and combined immature stages of *L. rufa* females generally occurred at higher temperatures compared to *L. brunnea* and *L. reticulatus* (Opit et al. 2010b). This observation further shows that *L. rufa* is adapted to surviving in relatively high temperature environments. Prior to ecological studies on *L. rufa*, the only two *Liposcelis* species that were known to survive well under relatively high temperatures were *Liposcelis paeta* (Wang et al. 2009) and *L. decolor* (Tang et al. 2008).

In its development from egg to adult, *L. reticulatus*, which is a parthenogenetic species, has four instars (Opit et al. 2010a). Exuviae consumption after molting has been found to be quite common in *L. reticulatus*. In the case of *L. rufa* and *L. brunnea*, which are described from both males and females, there were at least two different numbers of instars for males and three different numbers of instars for females; exuviae consumption

in these species is not as common as in *L. reticulatus*. In *L. reticulatus* where exuviae consumption is common, the general trend is that development is slower for psocids that did not eat exuviae. The possible reason for this could lie in the nutritional status of exuviae. Lipids and nitrogenous compounds (protein and chitin) can account for as much as 4.4% (Nelson and Sukkestad 1975) and 87% (Mira 2000), respectively, of the total weight of insect exuvia. Therefore, eating exuviae would be beneficial to psocids.

Effects of Temperature on Reproductive Parameters of L. reticulatus.

All reproductive parameters were found to vary with temperature. Intrinsic rate of population increase for *L. reticulatus* increased with temperature until 32.5°C (0.128) and then declined. If the intrinsic rate of increase at 32.5°C is considered the optimal fitness of 1, then the fitness of *L. reticulatus* at 22.5, 25, 27.5, 30, and 35°C equals 0.52, 0.70, 0.84, 0.87, and 0.84, respectively. Highest intrinsic rates of increase for *Liposcelis badia* (Jiang et al. 2008), *L. bostrychophila* (Wang et al. 2000), *L. decolor* (Tang et al. 2008), *L. paeta* (Wang et al. 2009), and *Liposcelis tricolor* Badonnel (Dong et al. 2007) occurred at 27.5, 30, 32.5, 32.5, and 30°C, respectively. Intrinsic rates of increase at these temperatures were 0.0455, 0.0946, 0.0609, 0.0542, and 0.0367, respectively. At optimal temperatures for intrinsic rate of increase, *L. reticulatus* has the highest potential for population growth among these psocid species.

All reproductive parameters varied with temperature (preoviposition period, oviposition period, postoviposition period, oviposition rate [eggs/female/wk], and longevity) and regression equations described the relationship between temperature and each of the reproductive parameters quite well (Opit et al. 2010a). *L. reticulatus*

oviposition period and longevity declined with increasing temperature (Opit et al. 2010a). A possible explanation for this may be that the higher egg maturation rates that occur at higher temperatures are associated with an overall higher metabolism which could reduce the life span (Papaj 2000, Jervis et al. 2005). At higher temperatures, they may also be allocating significantly more energy resources to egg production than maintenance of body functions thereby resulting in reduced performance and survival (Papaj 2000, Carey 2001, Jervis et al. 2005, 2007). It is plausible that at 22.5 and 35°C, *L. reticulatus* has a proportionately shorter egg laying period than at optimal temperatures because of the diversion of resources from egg production and maturation that may occur at these suboptimal temperatures, for example, resources could be diverted to maintenance of body functions other than reproduction.

Postoviposition periods for temperatures of 22.5, 25, and 27.5°C are longer than preoviposition periods; at temperatures of 30, 32.5, and 35°C they were either similar or shorter (Opit et al. 2010a). Preoviposition period declined with temperature most probably due to already stated reasons related to resource allocation, egg production, and egg maturation. Postoviposition also showed the same trend except there was an increase in the postoviposition period at 35°C for the same reasons.

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CHAPTER III

POPULATION GROWTH AND DEVELOPMENT OF THE PSOCID *LIPOSCELIS RUFA* (PSOCOPTERA: LIPOSCELIDIDAE) AT CONSTANT TEMPERATURES AND RELATIVE HUMIDITIES

(Journal of Economic Entomology, 2010, 103: 1920-1928)

Population Growth and Development of the Psocid *Liposcelis rufa* (Psocoptera: Liposcelididae) at Constant Temperatures and Relative Humidities

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Abstract

I investigated the effects of eight temperatures (22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, and 40.0°C) and four relative humidities (43, 55, 63, and 75%) on population growth and development of the psocid *Liposcelis rufa* Broadhead. *L. rufa* did not survive at 43% RH, at all temperatures tested; at 55% RH, at the highest four temperatures; and at 63% RH and 40.0°C. The greatest population growth was recorded at 35.0°C and 75% RH (73-fold growth). At 40.0°C, *L. rufa* populations declined or barely grew. *L. rufa* males have two to four nymphal instars, and the percentages of males with two, three, and four instars were 31, 54, and 15%, respectively. Female *L. rufa* have two to five instars, and the percentages of females with two, three, four, and five instars were 2, 44, 42, and 12%, respectively. The life cycle was shorter for males than females. I have developed temperature-dependent development equations for male and female eggs, individual nymphal, combined nymphal, and combined immature stages. The ability of *L. rufa* to reproduce at a relative humidity of 55% and temperatures of 22.5 to 30.0°C and at relative humidities of 63 to 75% and temperatures of 22.5 to 37.5°C, in addition to being able to survive at 40.0°C, suggests that this species would be expected to have a broader distribution than other *Liposcelis* species. These data provide a better understanding of *L. rufa* population dynamics and can be used to help develop effective management strategies for this psocid.

KEY WORDS Stored products, population growth, development rates, stored grain

Introduction

Psocids belonging to the genus *Liposcelis* (Psocoptera: Liposcelididae) increasingly pose a threat to stored products (Rees 1998). Before the 1990s in Australia and China and 2000s in the United States, psocids were not considered serious pests of stored products (Phillips and Throne 2010). However, in some countries such as Australia, they have now become the most frequently encountered stored-product pest in some areas (Rees 2003). Psocids infestations occur in grain storages on farms, collection centers, export terminals, warehouses with bagged commodities, and grain processing facilities worldwide. Heavy psocid infestations can lead to serious germ damage and significant weight losses in stored grain (Kučerová 2002) and they can cause health problems by transferring microorganisms and contaminating food materials with their feces and cast skins (Obr 1978, Sidik et al. 1986). The relative importance of psocids as stored-product pests has risen because of their varied response to management tactics that have been developed for beetle pests (Nayak et al. 1998, 2002a, 2002b, 2003; Nayak 2006) and the fact that markets increasingly view psocids as contaminants (Nayak 2006).

Psocid species known to infest stored grain in North America (Mockford 1993, Lienhard and Smithers 2002) are *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae), *Liposcelis bostrychophila* Badonnel (Psocoptera: Liposcelididae), *Liposcelis brunnea* Motschulsky, *Liposcelis corrodens* (Heymons), *Liposcelis decolor* (Pearman), *Liposcelis entomophila* (Enderlein), and *Liposcelis paeta* Pearman. In addition, *Liposcelis rufa* Broadhead has been found infesting wheat stored in steel bins in Stillwater, OK, USA (unpublished data).

There are no published studies on the biology of *L. corrodens* and *L. rufa*. However, development of an effective management program for any pest is dependent on having sound knowledge of its ecology. Given the lack of information on the ecology of *L. rufa*, I initiated studies on population growth and development of this species in order to provide an experimental basis for developing management strategies for this pest. My objectives were to determine the effects of constant temperatures and relative humidities on population growth of *L. rufa* and to quantify the effects of temperature on *L. rufa* development.

Materials and Methods

Insects. Cultures used in the study were started using insects collected from steel bins containing wheat located at the Stored Product Research and Education Center, Stillwater, OK. Voucher specimens of 100 male and female *L. rufa* preserved in 95% ethyl alcohol that were used in this study were deposited at K. C. Emerson Entomology Museum at Oklahoma State University under lot numbers 100 (males) and 101 (females). Psocids were reared on a mixture of 93% cracked hard red winter wheat, 5% rice krispies (Kellogg Company, Battle Creek, MI), and 2% wheat germ (wt/wt; referred to as psocid diet below) in 360-ml glass canning jars with mite-proof lids (Opit and Throne 2008), and the top 3 cm of the inner surface of each jar was coated with Fluon® (polytetrafluoroethylene; Northern Products, Woonsocket, RI) to prevent psocids accessing and gathering on the inside of the lid. Cultures were maintained at 30.0 ± 1°C and 75 ± 5% RH.

Effects of Temperature and Relative Humidity on Population Growth. I determined effects of temperature and relative humidity on the increase in number of psocids over a 30-d period at eight temperatures (22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, and 40.0°C) and four relative humidities (43, 55, 63, and 75%). The top third of the inner surface of 192 vials was coated with Fluon® to prevent psocids from escaping, and 5 g of cracked hard red winter wheat (*Triticum aestivum* L.) were placed in each vial. A screen (US #40 mesh) was placed in the snap-cap lid to allow air movement. Vials were randomly placed in each of four plastic boxes (42 by 29 by 24 cm high) containing saturated solutions of K_2CO_3, NaBr, $NaNO_2$, and NaCl below perforated false floors to maintain relative humidity (RH) of 43, 55, 63, and 75% (Greenspan 1977), respectively, and the cracked wheat in the vials was equilibrated for moisture content at room temperature for 4 wk.

One- to two-wk-old female *L. rufa* for the experiment were obtained by placing 0.5 g of colored psocid diet (Opit and Throne 2008), five particles of cracked wheat, 20 mg of wheat germ, and 40 adult female psocids of unknown age from the laboratory culture in each of one hundred and twenty 35-mm-diameter Petri dishes (Greiner Bio-One, Kaysville, UT), which had a coat of Fluon® on the inner walls to prevent psocids from escaping. Colored diet was used because *L. rufa* prefers laying eggs on and among diet particles, and colored diet makes it easier to see eggs and, therefore, make an assessment of whether sufficient numbers of eggs are being laid for the experiment. The Petri dishes were placed on false floors in three Rubbermaid plastic boxes (37 by 22 by 13 cm high) that contained saturated NaCl solution beneath false floors. The boxes had been painted black to exclude light and mimic dark conditions in which *L. rufa* is usually

found. Boxes were placed in an incubator maintained at 30.0 ± 1°C and 75 ± 5% RH. Psocids were removed from each Petri dish after 7 d, and the contents of 60 Petri dishes were poured into a 360-ml glass jar containing 80 g of psocid diet. The inner top part ('neck') of the jar had a coat of Fluon® and was closed using a mite-proof lid. The jar was placed back in the incubator. After 30 d, adult psocids found in the jar were approximately 1-2 wk old (based on preliminary work which indicated that development of females from egg to adult took approximately 23 d at 30.0°C).

Five 1- to 2-wk-old adult females were added to each of the 192 vials containing equilibrated diet, which were then incubated at each of the 32 temperature-RH combinations. Eight incubators were set at temperatures of 22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, and 40.0°C, where four plastic boxes (17 by 17 by 12 cm high) containing saturated solutions of K_2CO_3, NaBr, $NaNO_2$, and NaCl were placed. Six vials containing diet, equilibrated at room temperature and each relative humidity, were randomly assigned to the corresponding relative humidity box in all incubators. Four locations were established in every incubator for the boxes to occupy. Every 7 d, the boxes in each incubator were shuffled so that each box spent a total of at least 7 d in each location during the course of the experiment to counteract any temperature variability that may have existed in the incubators. During shuffling, the boxes were also checked to ensure that the salt solutions were still saturated; this was done by making sure that the desired amounts of the solute and solution of the saturated solution were present in each box. Environmental conditions in each incubator were monitored using a temperature and RH sensor (HOBO U12, Onset Computer Corporation, Bourne, MA). Live insects in each vial were counted after 30 d by spreading a portion of the contents of a vial on a 9-cm

Petri dish, which had a coat of Fluon® on the inner walls, and removing all motile *L. rufa* using a moist brush under a stereomicroscope (Zeiss Stemi 2000-C; Thornwood, NY, USA).

The experiment had three temporal replications, and the experimental design was a randomized complete block (RCBD) with sub sampling. All statistical procedures were accomplished using Statistical Analysis System software (SAS Institute 2001). PROC MIXED was used for analysis of variance (ANOVA) to determine the effects of temperature and relative humidity on numbers of psocids in vials, which were transformed using the square-root transformation to stabilize variances before analysis. Untransformed means and standard errors are reported to simplify interpretation. Least significant difference (LSD) test was used to determine differences among mean numbers of psocids produced at different temperatures and relative humidities, despite the quantitative independent variables, because I was not able to quantify the relationship using a biologically meaningful equation (Table Curve 3D) (Systat Software, Inc. 2002b). A biologically meaningful equation is a mathematical expression that adequately describes a relationship in a biologically-meaningful way.

Effects of Temperature on Development. The procedures used for setting up the experiment were analogous to those used by Opit and Throne (2008) except each vial cap had three cracked wheat kernels. Thirty centrifuge caps containing eggs were then randomly placed in each of eight plastic boxes (37 by 22 by 13 cm high) that were painted black and contained saturated NaCl solution to maintain 75% RH. One box was placed in each of eight incubators set to maintain treatment temperatures of 22.5, 25.0, 27.5, 30.0, 32.5, 35.0, 37.5, and 40.0°C. The procedures for monitoring egg and nymphal

development were similar to those used by Opit and Throne (2008) where psocids were marked using fluorescent powder. The experiment consisted of three temporal replications.

In the determination of the effects of temperature on the duration of development of *L. rufa*, data for males and females were analyzed separately. For both data sets, the design used for analysis was a RCBD with sub sampling. PROC MIXED was used for ANOVA to determine the effects of temperature on development. Regression (TableCurve 2D) (Systat Software, Inc. 2002a) was used to describe the relationship between temperature and development time for the egg, individual nymphal, combined nymphal, and combined immature stages of males and females. Selection of an equation to describe the data was based on the magnitude and pattern of residuals, lack-of-fit tests, and whether the curve had a shape that was reasonable for describing the data. In the analysis of the proportions of viable eggs and nymphs that developed to the adult stage (male plus female), the design for analysis was a RCBD. To analyze these proportions, PROC GLM was used for ANOVA after arcsine square-root transformation to stabilize variances. Least significant difference (LSD) test was used to determine differences among proportions of nymphs that survived to adult at different temperatures, despite the quantitative independent variable, because I was not able to quantify the relationship using a biologically meaningful equation (TableCurve 2D) (Systat Software, Inc. 2002a).

The lower development threshold for *L. rufa* males and females was determined by fitting linear equations to development rate (reciprocal of development time) and temperature data using TableCurve 2D (Systat Software, Inc. 2002a). Because the rate of development varies when temperatures become suboptimal for development, data were

only fit to linear regression within the linear portion of the curve (Arnold 1959). Therefore, for both males and females, 40.0°C data were not used for linear regression. Upper development thresholds for *L. rufa* males and females were found by determining the temperature at which the rate of development begins to decrease (Zilahi-Balogh and Pfeiffer 1998); these temperatures were obtained by fitting the appropriate equation to all the development rate and temperature data and using the 'EVALUATE' procedure in TableCurve 2D (Systat Software, Inc. 2002a) to determine upper development threshold.

Results

Effects of Temperature and Relative Humidity on Population Growth. The pattern of psocid numbers at the eight temperatures was not similar at the four relative humidities ($F = 22.4$; df = 21,62; and $P < 0.01$). No live *L. rufa* were found in treatments maintained at 43% RH; at 55% RH at the four highest temperatures tested; and at 63% RH at 40.0°C (Table 1). Population growth at 30.0, 32.5, and 35.0°C and 63% RH, and at 30.0, 32.5, 35.0, and 37.5°C and 75% RH was higher than that at other treatments. Population growth at 32.5 and 37.5°C and 75% RH was similar (64- and 60-fold, respectively, were recorded). Numbers of *L. rufa* increased most rapidly at 35.0°C and 75% RH where the average increase in population was 73-fold (Table 1). At 40.0°C, *L. rufa* populations declined or barely grew. *L. rufa* appears capable of surviving under a wide range of conditions ranging from 22.5 to 40.0°C and 55% to 75% RH.

Effects of Temperature on Male Development. *Eggs.* Incubation time varied with temperature, and a quadratic equation described the relationship between temperature and incubation time well (Fig. 1A, Tables 2 and 3). Based on the quadratic

equation, the predicted optimal incubation temperature is 36.3°C, and development is completed in 6.3 d at this temperature.

Nymphal, Combined Nymphal, and Combined Immature Stages. Duration of the nymphal, combined nymphal, and combined immature stages varied with temperature (Figs. 1B-F; Tables 2 and 3). Quadratic equations described the relationship between temperature and development time well for nymphal, combined nymphal, and combined immature stages (Table 3). Based on the quadratic equations for N1, N2, and N3, the predicted optimal development temperatures are 35.7, 37.0, and 35.3°C, and development is completed in 5.4, 4.5, and 3.9 d, respectively. For the combined nymphal and combined immature stages, these parameters are 34.8 and 35.3°C, and 11.6 and 16.8 d, respectively. The lower development threshold for the combined immature stage was estimated as 12.2°C using a linear equation; the upper development threshold for the combined immature stage was estimated as 36.9°C using a quadratic equation. The linear and quadratic equations described the development rate and temperature data well (Table 4).

Effects of Temperature on Female Development. *Eggs.* Incubation time varied with temperature and a quadratic equation described the relationship between temperature and incubation time well (Fig. 2A, Tables 5 and 6). Based on the quadratic equation, the predicted optimal incubation temperature is 37.3°C, and development is completed in 4.7 d at this temperature.

Nymphal, Combined Nymphal, and Combined Immature Stages. Duration of the nymphal, combined nymphal, and combined immature stages varied with temperature

(Figs. 2B-D and 3A-C; Tables 5 and 6). Quadratic equations described the relationship between temperature and development time well for nymphal, combined nymphal, and combined immature stages (Table 6). Based on the quadratic equations for N1, N2, N3, and N4, the predicted optimal development temperatures are 35.2, 35.0, 40.0, and 36.5°C, and development is completed in 5.3, 4.7, 4.2, and 4.9 d, respectively. For the combined nymphal and combined immature stages, these parameters are 35.1 and 35.8°C, and 16.1 and 21.0 d, respectively. The lower development threshold for the combined immature stage was estimated as 8.5°C using a linear equation; the upper development threshold for the combined immature stage was estimated as 38.7°C using a quadratic equation. The linear and quadratic equations described the development rate and temperature data well (Table 4).

Effects of Temperature on Egg Viability and Nymphal Survivorship.

Temperature had no effect on egg viability ($F = 0.9$; df = 7,14; $P = 0.52$). The proportion of viable eggs for all temperatures ranged from 0.85 to 0.95 and averaged 0.90 over all temperatures. Nymphal survivorship at temperatures of 22.5 to 37.5°C ranged from 0.76 to 0.91 and averaged 0.84. However, survivorship was lower at 40.0°C where the proportion of nymphs surviving was only 0.34 (Table 7).

The mean developmental period of females was longer than that of males. This corresponded to females generally having one more instar than the males (Tables 2 and 5). I found that male *L. rufa* have two to four nymphal instars, and the percentages of males with two, three, and four instars were 31, 54, and 15%, respectively. Female *L. rufa* were found to have two to five nymphal instars, and the percentages of females with two, three, four, and five instars were 2, 44, 42, and 12%, respectively.

Discussion

My data show that *L. rufa* will not survive at 43% RH, in the temperature range of 22.5 to 40.0°C; at 55% RH, in the temperature range of 32.5 to 40.0°C; and at 63% RH at 40.0°C. The optimal relative humidity for population growth is 75%. The inability of stored-product psocid pests to survive at 43% RH was also demonstrated for *L. reticulatus* (Opit and Throne 2008) and *L. brunnea* (Opit and Throne 2009). The ability of *L. rufa* to multiply at 55% RH, in the temperature range of 22.5 to 30.0°C, seems to indicate that it is better adapted to surviving under low humidity conditions compared to some other *Liposcelis* species. For example, Weng (1986) showed that mortality of adult female *L. entomophila* increased sharply at humidities below 56% and Rees and Walker (1990) found that none of the three psocid species they studied (*L. bostrychophila, L. entomophila*, and *L. paeta*) were able to survive at relative humidities below 60%. The fact that *L. entomophila* in one study did not survive below 60% RH and yet did so in another study, may be due to differences in the geographical strains used in the two studies. Besides *L. rufa*, *L. brunnea* is also capable of reproducing at 55% RH, in the temperature range of 22.5 to 32.5°C (Opit and Throne 2009). In fact, at the 22.5 to 27.5°C temperature range, the reproduction rate of *L. brunnea* is much higher than that of *L. rufa* at 55% RH (Opit and Throne 2009). Psocids maintain body water levels by absorbing atmospheric water vapor when RH is 60% or above; however, below this level, more water is lost than gained resulting in dehydration and death (Devine 1982). Therefore, it is likely that *L. rufa* and *L. brunnea* are adapted in a manner that enables them to absorb atmospheric water vapor when relative humidity is as low as 55%.

The highest population increase for *L. rufa* occurred at 35.0°C and 75% RH; generally reproduction was higher at 75% RH. Optimal humidities for *L. entomophila* (Wang et al. 1998) and *L. reticulatus* (Opit and Throne 2008) were similar, 80-90% and 75%, respectively. However, Opit and Throne (2009) found that the optimal humidity for *L. brunnea* was 63%; in fact, population increase at 55% was not different from that at 63% in the 22.5 to 30.0°C range. This would seem to indicate that *L. brunnea* would be expected to have a much broader distribution than *L. entomophila* and *L. reticulatus* and would be found in relatively dry habitats as well. As a matter of fact, *L. brunnea* occurs commonly throughout the dry parts of United States (Mockford 1993). Because *L. brunnea* will not survive at temperatures of 35.0°C or higher (Opit and Throne 2009), high temperatures appear to limit its distribution. Despite being adapted to higher temperatures (37.5°C) and relative humidities (75%), *L. rufa* also survives and reproduces relatively well at 55 and 63% RH and temperatures as low as 22.5 and 25.0°C. This would imply that *L. rufa* would be expected to have an even broader distribution than *L. brunnea*. Based on my data, *L. rufa* is capable of surviving at 40.0°C; however, its population will either decline or barely grow at this high temperature. This observation may be partly explained by the fact that only 34% of the nymphs are able to develop to adult at 40.0°C. Prior to the present study, the only two *Liposcelis* species that were known to survive and reproduce well under relatively high temperatures (≥ 37.5°C) were *L. decolor* (Tang et al. 2008) and *L. paeta* (Wang et al. 2009).

I found that 58 to 71% of total nymphal mortality was due to N1 and N2 mortality. This mortality is lower than that for *L. reticulatus* (80-100%) (Opit and Throne 2008) and *L. brunnea* (87-100%) (Opit and Throne 2009). A possible explanation for this

could be that *L. rufa* nymphs are much hardier and cope much better with the handling they are exposed to during experiments. In addition, the relative humidity in which the nymphs developed (75%) is the optimal relative humidity for *L. rufa*, hence the reduced mortality. The high mortality in the case of *L. brunnea* may be due to the 75% RH in which nymphal development was studied. The optimal relative humidity for *L. brunnea* is 63%. *L. rufa* nymphal survivorship at temperatures of 22.5 to 37.5°C ranged from 76% to 91% and averaged 84%. As already mentioned, survivorship was lower at 40.0°C where only 34% of the nymphs survived.

The developmental period of female *L. rufa* was longer than that of males. This corresponded to females generally having one more instar than males. According to Mockford (1993), insects in the order Psocoptera usually have four to six nymphal stages. However, my study shows that male *L. rufa* have two to four instars, and the percentages of males with two, three, and four instars were 31, 54, and 15%, respectively. I have also shown that female *L. rufa* have two to five instars, and the percentages of females with two, three, four, and five instars were 2, 44, 42 and 12%, respectively. In comparison with *L. brunnea* (Opit and Throne 2009), both species have two to four male instars and proportionately more of them have three instars. In the case of females, proportionately more *L. brunnea* have four instars whereas a higher proportion of *L. rufa* females have three and four instars.

At 75% RH, the optimal temperature for development of *L. rufa* from egg to adult is 37.5°C and at this temperature development is completed in 21.6 d. At the same RH, the optimal temperature for the development of *L. badia* Wang, Wang, and Lienhard (Jiang et al. 2008), *L. bostrychophila* (Wang et al. 2000), *L. brunnea* (Opit and Throne

2009), *L. reticulatus* (Opit and Throne 2008), and *L. tricolor* Badonnel (Dong et al. 2007) was 32.5°C; at this temperature development is completed in 17.2, 18.1, 30.5, 22.9, and 30.7 d, respectively. In the case of *L. entomophila* (Wang et al. 1998), *L. decolor* (Tang et al. 2008), and *L. paeta* (Wang et al. 2009), the optimal temperatures are 35.0, 35.0, and 37.5°C and development is completed in 21.7, 16.1, and 11.5 d, respectively. This suggests that *L. decolor*, *L. entomophila*, *L. paeta*, and *L. rufa* with higher optimal temperatures for development will probably occur commonly in warmer environments. In fact, this observation may also explain why these species are commonly found in large numbers in grain storages where temperatures get quite high during warmer periods of the year. The development time of *L. rufa* under optimal conditions is similar to that of two major stored-product beetle pests, namely, *R. dominica* (F.) (Coleoptera: Bostrichidae) and *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae). Under optimal conditions of 34.0°C and 70% RH, *R. dominica* completes development in 25 d whereas *T. castaneum* completes development in 20 d under optimal conditions of 35.0 to 37.5°C and > 70% RH (Rees 2004).

Quadratic equations describe the relationship between temperature and development time for the various stages of male and female *L. rufa* well. Similar results were found by Wang et al. (2000) in their study on the biology of *L. bostrychophila* and by Opit and Throne (2008, 2009) in their studies on the biology of *L. reticulatus* and *L. brunnea*. This relationship between temperature and development time is a result of the inability of ectotherms (such as psocids) to regulate their body temperature, thus body temperature is a function of the temperature of their surroundings, such that within a certain range, the rate of metabolic reactions will be directly related to temperature

(Speight et al. 1999). Beyond optimal temperatures for development, temperature negatively impacts biological processes and results in increased development time. It is important to state that the predictive accuracy of the equations I developed may be reduced by the fact that the number of observations taken at 40.0°C was small due to high mortality that occurs at this temperature. Notwithstanding, for female *L. rufa*, the predicted optimal temperatures for egg, combined nymphal, and combined immature stage development, are 37.3, 35.1, and 35.8°C, respectively. At these temperatures, development is completed in 4.7, 16.1, and 21.0 d, respectively.

Based on my data, the lower and upper developmental thresholds for *L. rufa* males are 12.2 and 36.9°C, respectively; for females, these temperatures are 8.5 and 38.7°C, respectively. My results show that the lower developmental threshold for *L. rufa* females is lower than that for *L. bostrychophila* (Wang et al. 2000), *L. tricolor* (Dong et al. 2007), *L. badia* (Jiang et al. 2008), and *L. paeta* (Wang et al. 2009), which are 15.5, 11.3, 10.0, and 20.2°C , respectively, but that for males is similar to these. The upper developmental thresholds for both male and female *L. rufa* are similar to those of the aforementioned *Liposcelis* species which were 38.8 (Wang et al. 2000), 38.9 (Dong et al. 2007), 40.0 (Jiang et al. 2008), and 40.4°C (Wang et al. 2009), respectively. The lower and upper developmental thresholds I have developed for *L. rufa* are important for integrated management of this pest (Briere et al. 1999) because they can be used to reliably predict its population dynamics.

Despite my expectations that *L. rufa* would be broadly distributed and a major pest in areas with hot and humid climate, this does not seem to be the case as this is only the second report of this insect in stored grain, to the best of my knowledge. The first

case was a report of *L. rufa* as a new stored product pest species found in stored rice in Portugal (Kučerová et al. 2006). Possible reasons for why broader occurrence of *L. rufa* has not been reported in hot and humid climates are that the species has not been well investigated and it has probably been misidentified.

My work has shown that *L. rufa* can reproduce at a relative humidity of 55% and temperatures of 22.5 to 30.0°C and at relative humidities of 63 to 75% and temperatures of 22.5 to 37.5°C. In addition, it's capable of surviving at 40.0°C. The optimal conditions for reproduction for this species are 35.0°C and 75% RH. I have also shown that males have two to four instars whereas females have two to five instars. Given the short life cycle of *L. rufa* and its ability to multiply rapidly at high temperatures and relative humidities, *L. rufa* would be expected to be a serious stored product pest in hot and humid climates. Also, I would expect it to have a broader distribution than other *Liposcelis* species because it can reproduce at 55% RH. Finally, temperature-dependent development equations I have developed can be used to elucidate *L. rufa* population dynamics and to help develop effective management strategies.

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Table 1. Final number (± SE) of motile *Liposcelis rufa* present in vials after 30 d (n = 18).

Temperature (°C)	Relative humidity (%)			
	43	55	63	75
22.5	0.0 ± 0.0a	15.6 ± 2.01b	38.1 ± 4.00e	27.0 ± 3.63d
25	0.0 ± 0.0a	12.9 ± 2.34b	75.8 ± 7.29g	60.8 ± 6.78f
27.5	0.0 ± 0.0a	13.1 ± 2.01b	80.1 ± 6.31g	70.4 ± 7.65fg
30	0.0 ± 0.0a	58.4 ± 6.95f	144.6 ± 15.79h	138.4 ± 17.48h
32.5	0.0 ± 0.0a	0.0 ± 0.0a	251.5 ± 37.02i	323.9 ± 23.36jk
35	0.0 ± 0.0a	0.0 ± 0.0a	130.8 ± 20.06h	363.4 ± 32.88k
37.5	0.0 ± 0.0a	0.0 ± 0.0a	17.7 ± 7.56bc	300.7 ± 24.49j
40	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	2.7 ± 1.25a

Means followed by the same letter are not significantly different.

Table 2. Duration (d ± SE) of immature stages of male *Liposcelis rufa* at eight constant temperatures and 75% RH.

Temperature (°C)		Duration (d)					
	n	Eggs	N1	N2	N3[a]	Nymphs	Eggs + nymphs
22.5	24	15.6 ± 0.22	7.9 ± 0.26	7.3 ± 0.35	7.2 ± 0.33	27.7 ± 0.67	43.4 ± 0.70
25	34	11.6 ± 0.19	7.8 ± 0.22	6.1 ± 0.29	5.7 ± 0.28	21.1 ± 0.56	32.6 ± 0.59
27.5	33	8.8 ± 0.19	6.3 ± 0.23	5.8 ± 0.31	5.4 ± 0.29	18. 1 ± 0.59	26.9 ± 0.62
30	29	7.5 ± 0.18	5.8 ± 0.24	4.5 ± 0.32	4.0 ± 0.41	13.1 ± 0.62	20.6 ± 0.65
32.5	38	6.4 ± 0.18	4.9 ± 0.22	4.8 ± 0.29	5.0 ± 0.52	11.5 ± 0.55	17.8 ± 0.58
35	21	5.1 ± 0.24	5.9 ± 0.28	5.1 ± 0.38	3.4 ± 0.65	12.7 ± 0.72	17.9 ± 0.76
37.5	31	5.3 ± 0.20	5.8 ± 0.24	4.5 ± 0.31	3.8 ± 0.44	12.3 ± 0.61	17.5 ± 0.63
40	13	5.8 ± 0.31	5.3 ± 0.37	4.3 ± 0.49	4.5 ± 0.54	14.2 ± 0.94	19.9 ± 0.98

ANOVA results for egg, N1, N2, N3, combined nymphal, and combined immature stages were F = 275.1, 4.3, 8.7, 11.2, 63.8 and 130.7 respectively. In all cases df = 7,14 and $P < 0.01$.

[a] Values of n for N3 at 30, 32.5, 35, 37.5, and 40°C were 19, 12, 10, 14, and 9, respectively.

Table 3. Parameters (± SE) for quadratic equations describing the duration of the egg, individual nymphal, combined nymphal, and combined immature stages of male *Liposcelis rufa* at constant temperatures.

Subject	Maximum R^2	Adjusted R^2	*F*	a	b	c
Egg duration	0.99	0.98	663.3	74.68 ± 3.13	-3.83 ± 0.2051	0.0527 ± 0.0033
N1 duration	0.61	0.43	10.5	26.24 ± 6.96	-1.17 ± 0.4563	0.0164 ± 0.0073
N2 duration	0.77	0.67	21.8	21.77 ± 4.59	-0.934 ± 0.3011	0.0126 ± 0.0048
N3 duration	0.60	0.43	10.7	28.55 ± 7.76	-1.396 ± 0.5084	0.0198± 0.0081
Nymphal duration	0.92	0.89	101.7	138.92 ± 12.25	-7.319 ± 0.802	0.1052± 0.0128
Egg + nymphal duration	0.97	0.96	270.2	214.67 ± 12.44	-11.212 ± 0.81	0.1588 ± 0.0130

N1, N2 and N3 represent the 1^{st}, 2^{nd}, and 3^{rd} instars, respectively.

In all cases df = 2,21 and $P < 0.001$. Lack-of-fit *P*-values for the duration of the egg, N1, N2, N3, combined nymphal, and combined immature stages were 0.06, 0.51, 0.29, 0.62, 0.65, and 0.75 respectively.

Table 4. Parameters (± SE) for linear and quadratic equations describing the effects of constant temperatures on the development rate of the combined immature stage of *Liposcelis rufa* males and females.

Subject	Maximum R^2	Adjusted R^2	*F*	a	b	c
Males*	0.94	0.87	127.2	-0.0305 ± 0.0067	0.0025 ± 0.0022	-
Females*	0.85	0.74	54.5	-0.0145 ± 0.0070	0.0017 ± 0.0023	-
Males	0.91	0.85	70.6	-0.189 ± 0.034	0.0135 ± 0.0022	-0.0002 ± 0.00004
Females	0.84	0.77	41.7	-0.112 ± 0.032	0.0083 ± 0.0021	-0.0001 ± 0.00003

In cases with an asterisk (*), an R^2 value is presented. For both linear equations, df = 1,19 and $P < 0.001$. Lack-of-fit *P*-values for males and females were 0.06 and 0.13, respectively. For both quadratic equations, df = 2,21 and $P < 0.001$. Lack-of-fit *P*-values for males and females were 0.35 and 0.55, respectively.

Table 5. Duration (d ± SE) of immature stages of female *Liposcelis rufa* at eight constant temperatures and 75% RH.

Temperature (°C)		Duration (d)						
	n	Eggs	N1	N2	N3[a]	N4[b]	Nymphs	Eggs+nymphs
22.5	24	14.2 ± 0.25	10.0 ± 0.32	6.8 ± 0.37	7.1 ± 0.38	7.4 ± 0.45	33.2 ± 0.93	47.4 ± 0.96
25	32	10.2 ± 0.22	7.6 ± 0.28	6.0 ± 0.34	6.4 ± 0.34	6.4 ± 0.44	27.0 ± 0.84	37.3 ± 0.87
27.5	35	8.4 ± 0.20	6.4 ± 0.26	5.5 ± 0.31	5.0 ± 0.31	5.6 ± 0.50	21.1 ± 0.77	29.5 ± 0.79
30	42	6.67 ± 0.18	5.8 ± 0.23	4.3 ± 0.28	4.7 ± 0.28	5.3 ± 0.59	17.2 ± 0.69	24.5 ± 0.72
32.5	32	5.7 ± 0.23	5.2 ± 0.30	4.6 ± 0.35	4.6 ± 0.36	4.7 ± 0.88	15.9 ± 0.88	21.7 ± 0.91
35	37	5.1 ± 0.20	6.1 ± 0.25	5.8 ± 0.29	5.2 ± 0.31	5.8 ± 0.63	19.4 ± 0.74	24.6 ± 0.76
37.5	29	5.0 ± 0.22	5.9 ± 0.29	4.3 ± 0.34	4.9 ± 0.35	4.7 ± 0.88	16.6 ± 0.84	21.6 ± 0.87
40	9	4.5 ± 0.50	5.3 ± 0.63	4.9 ± 0.74	3.5 ± 0.75	4.8 ± 0.97	17.4 ± 1.84	22.0 ± 1.91

ANOVA results for egg, N1, N2, N3, N4, combined nymphal, and combined immature stages were $F = 91.8$, $P < 0.0001$; $F = 8.1$, $P = 0.0005$; $F = 5.2$, $P = 0.0043$; $F = 3.3$, $P = 0.0281$; $F = 3.4$, $P = 0.0245$; $F = 23.6$, $P < 0.0001$; and $F = 46.3$, $P < 0.0001$, respectively; in all cases df = 7,14.

[a] Values of n for N3 at 35 and 37.5°C were 34 and 28 respectively.

[b] Values of n for N4 at 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C were 23, 27, 20, 17, 10, 17, 10, and 6 respectively.

Table 6. Parameters (± SE) for quadratic equations describing the duration of the egg, individual nymphal, combined nymphal, and combined immature stages of female *Liposcelis rufa* at constant temperatures.

Subject	Maximum R^2	Adjusted R^2	*F*	a	b	c
Egg duration	0.98	0.96	285.3	62.07 ± 4.31	-3.08 ± 0.287	0.0413 ± 0.0045
N1 duration	0.77	0.65	23.6	37.815 ± 6.83	-1.846 ± 0.447	0.0262 ± 0.0071
N2 duration	0.65	0.34	7.8	20.879 ± 5.78	-0.924 ± 0.378	0.0132 ± 0.0060
N3 duration	0.54	0.33	7.5	17.969 ± 7.98	-0.676 ± 0.523	0.0083 ± 0.0083
N4 duration	0.59	0.40	9.8	20.782 ± 6.02	-0.869 ± 0.394	0.0119 ± 0.0063
Nymphal duration	0.87	0.79	45.9	145.12 ± 19.14	-7.359 ± 1.254	0.1049 ± 0.020
Egg + nymphal duration	0.94	0.89	99.0	204.69± 20.22	-10.26 ± 1.32	0.1434 ± 0.0211

N1, N2, N3, and N4 represent the 1^{st}, 2^{nd}, 3^{rd}, and 4^{th} instars, respectively;

In all cases df = 2,21 and $P < 0.001$.

Lack-of-fit *P*-values for the duration of the egg, N1, N2, N3, N4, combined nymphal, and combined immature stages were 0.09, 0.37, 0.13, 0.55, 0.55, 0.27, and 0.23 respectively.

Table 7. Proportion of *Liposcelis rufa* nymphs (± SE) surviving to adult.

Temperature (°C)	Proportion of nymphs surviving to adult
22.5	0.76 ± 0.03c
25	0.90 ± 0.01a
27.5	0.86 ± 0.03abc
30	0.91 ± 0.03a
32.5	0.88 ± 0.04ab
35	0.78 ± 0.02bc
37.5	0.82 ± 0.04abc
40	0.34 ± 0.08d

ANOVA results for proportion of nymphs surviving were $F = 16.6$; df = 7,14; and $P < 0.01$.

Means within the column followed by the same letter are not significantly different.

List of Figures

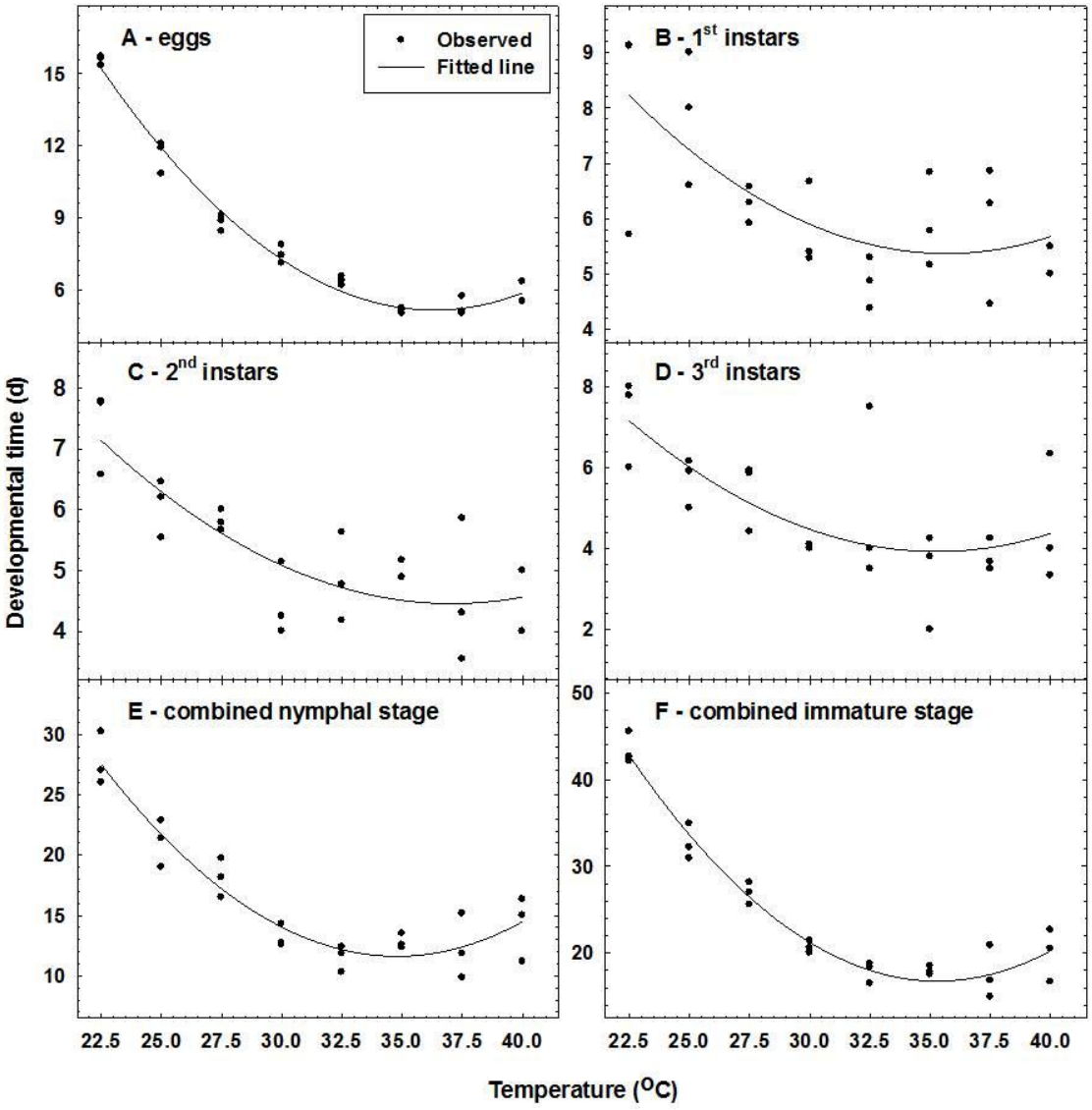
A - eggs
Observed
Fitted line
B - 1st instars
C - 2nd instars
D - 3rd instars
E - combined nymphal stage
F - combined immature stage
Developmental time (d)
Temperature (°C)
22.5
25.0
27.5
30.0
32.5
35.0
37.5
40.0

Fig. 1.

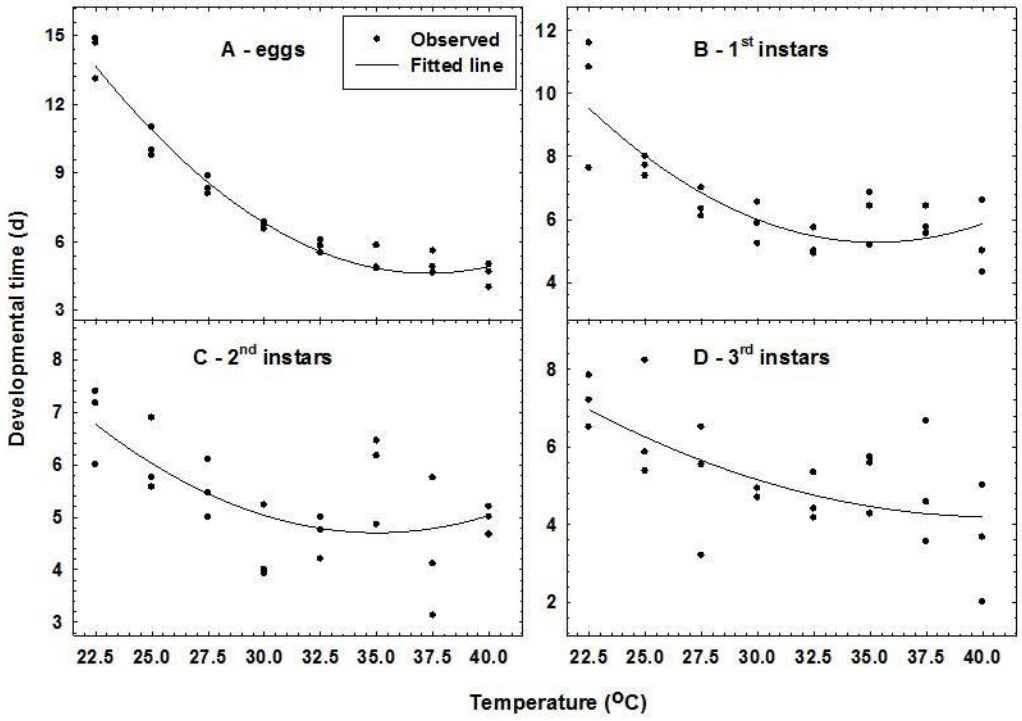
A - eggs
Observed
Fitted line
B - 1st instars
C - 2nd instars
D - 3rd instars
Developmental time (d)
Temperature (°C)
22.5 25.0 27.5 30.0 32.5 35.0 37.5 40.0

Fig. 2

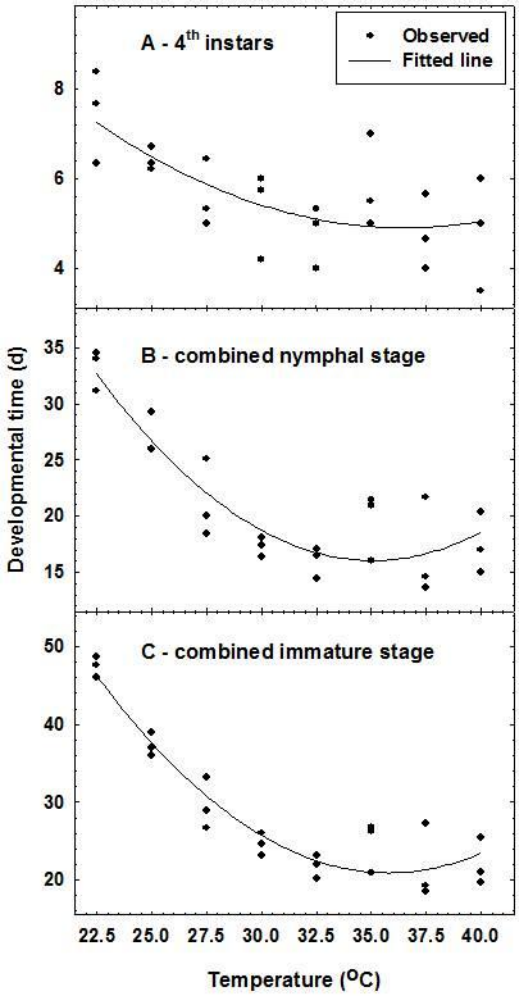
A - 4th instars
Observed
Fitted line
B - combined nymphal stage
C - combined immature stage
Developmental time (d)
Temperature (°C)
22.5
25.0
27.5
30.0
32.5
35.0
37.5
40.0

Fig. 3.

CHAPTER IV

REPRODUCTIVE PARAMETERS OF THE PSOCID *LIPOSCELIS RUFA* (PSOCOPTERA: LIPOSCELIDIDAE) AT CONSTANT TEMPERATURES

(To be submitted to Journal of Economic Entomology)

Abstract

The effects of seven temperatures on the reproductive parameters of the psocid *Liposcelis rufa* Broadhead (Psocoptera: Liposcelididae) were investigated at 75% RH. Peak oviposition rates (eggs/female/wk) at temperatures of 25, 27.5, 30, 32.5, 35, 37.5, and 40.0°C were 8.2, 10.9, 13.7, 14.7, 15.4, 13.8, and 8.7, respectively. At these temperatures, *L. rufa* laid 60, 64, 71, 88, 89, 94 and 94%, respectively, of the total number of eggs in the first four weeks. Mean weekly oviposition rate increased with temperature and was highest at 35°C (4.7 eggs/female/wk). The longest preoviposition and postoviposition periods were observed at 25°C and were 2.5 d and 42.9 d, respectively. Oviposition period and longevity decreased with increasing temperature - at 25°C, these parameters were 93 and 139 d, respectively, and at 40°C, they were 26 and 36 d, respectively. The longest lived individuals lived for 32, 32, 22, 15, 17, 12, and 9 wk at 25, 27.5, 30, 32.5, 35, 37.5, and 40°C, respectively. Intrinsic rate of population increase increased with temperature until 32.5°C (0.18) and then declined. The temperature-dependent equations that I have developed for preoviposition, postoviposition, and oviposition periods, oviposition rate, fecundity, longevity, and percentage of life spent in oviposition can be used in simulation models to predict *L. rufa* population dynamics for the development of effective management strategies.

KEY WORDS Stored products, longevity, fecundity, oviposition period, stored grain

Psocids of the genus *Liposcelis* (Psocoptera: Liposcelididae) have risen to prominence as serious pests of stored-product commodities all over the world (Rees 1998, Nayak 2006, Throne et al. 2006) in the last two decades. Prior to 1990s in Australia and China and 2000s in the United States, psocids were not considered as pests (Phillips and Throne 2010). In some parts of countries such as Australia, they have now become the most frequently encountered storage pests in some areas (Rees 2003). Differential response of psocids to commonly used residual insecticides and the fumigant phosphine (Nayak et al. 1998, Nayak 2006, Nayak and Collins 2008); the economic losses they cause by feeding on germ and endosperm (Kučerová 2002a); the deterioration in quality of stored products they cause through the presence of live and dead specimens, exuviae, and feces (Obr 1978); and the fact that markets increasingly view psocids as contaminants (Nayak 2006) have contributed to the worldwide recognition of psocids as pests of stored-product commodities.

Fifteen out of sixteen species of Psocoptera that are considered pests of stored products are found in the United States (Ahemdani et al. 2010). However, not all are reported as pests. For example, *Liposcelis rufa* Broadhead, recently found infesting stored wheat in Oklahoma (Gautam et al. 2010), was previously reported from Hawaii (Mockford and Krushelnycky 2008), but was not considered a pest then. Psocid species known to infest stored grain in North America (Mockford 1993, Lienhard and Smithers 2002) are *Lepinotus reticulatus* Enderlein (Psocoptera: Trogiidae), *Liposcelis bostrychophila* Badonnel, *Liposcelis brunnea* Motschulsky, *Liposcelis corrodens* Heymons, *Liposcelis decolor* (Pearman), *Liposcelis entomophila* (Enderlein), and *Liposcelis paeta* Pearman. In addition, *L. rufa* has been found infesting stored wheat in

Oklahoma (Gautam et al. 2010). Prior to this, *L. rufa* had also been found in stored rice in Portugal (Kučerová 2006) and in imported wood in Australia (Rees 2008). It is very likely that *L. rufa* has been infesting stored commodities for a long time before these preceding recent reports.

Until recently, there was no published information on the biology and ecology of *L. rufa*. However, development of an effective management program for any pest is dependent on having sound knowledge of its ecology. Therefore, Gautam et al. (2010) studied the effects of temperature and relative humidity on population growth and development of *L. rufa* over a range of temperatures and relative humidities. They found that *L. rufa* may have a broader ecological distribution compared to other *Liposcelis* spp. because it can survive and multiply at 55% RH at temperatures of 22.5 to 30°C and at temperatures as high as 40°C, at 75% RH. They also developed temperature dependent developmental equations to elucidate *L. rufa* population dynamics. However, there are currently no published studies on the effects of temperature on the reproductive parameters of *L. rufa*. Reproductive parameters affect population dynamics, and information on these parameters can be used in simulation models to predict *L. rufa* population dynamics. Therefore, the objective of the present study is to determine the reproductive parameters of this species over a range of temperatures.

Materials and Methods

Insects. Cultures used in this study were started with insects collected from steel bins containing wheat (*Triticum aestivum*) located at the Stored Product Research and Education Center, Stillwater, OK. Voucher specimens of 100 male and female *L. rufa* preserved in 95% ethyl alcohol that were used for this study were deposited at K. C.

Emerson Entomology Museum at Oklahoma State University under lot numbers 100 (males) and 101 (females). Psocids were reared on a mixture of cracked hard red winter wheat, rice krispies (Kellogg Company, Battle Creek, MI), and wheat germ (93, 5, and 2% wt/wt: referred to as psocid diet hereafter) in 360-ml glass canning jars with mite-proof lids (Opit and Throne 2008a). The inner top one third portion of the glass jar was coated with Fluon® (polytetrafluoroethylene; Northern Products, Woonsocket, RI) to prevent psocids from gathering on the lids. The cultures were maintained at 30 ± 1°C and 75 ± 5% RH.

Obtaining 1- to 2-Week-Old Adults. One to two-wk-old female *L. rufa* were obtained by placing 0.5 g of colored psocid diet (Opit and Throne 2008b), five particles of cracked wheat, 20 mg of wheat germ, and 30 adult females from the laboratory cultures in each of two hundred 35-mm-diameter Petri dishes (Greiner Bio-One, Kaysville, UT). The inner walls of the Petri dishes were coated with Fluon® to prevent psocids from escaping. Colored diet was used as substrate for laying eggs because *L. rufa* prefers laying on and among diet particles, which makes it easier to determine the number of eggs being laid for the experiment. The Petri dishes were placed on false floors in four Rubbermaid plastic boxes (37 by 22 by 13 cm in height) which contained saturated NaCl beneath their false floors to maintain 75 ± 5% RH (Greenspan 1977). The plastic boxes used for the experiment were painted black to exclude light and mimic dark conditions in which *L. rufa* is usually found. The boxes were then kept in 30 ± 1°C. After seven days, all live females from each Petri dish were removed using a moist brush and the contents of fifty Petri dishes were poured in a 360-ml glass jar containing 80 g of psocid diet. The inner one third portion of each jar was coated with Fluon® and closed

using a mite proof lid. The jars were returned to the incubator (30 ± 1°C and 75 ± 5% RH). After 30 days, adult females found in the jars were approximately 1-2 wk old (Gautam et al. 2010).

***Obtaining Freshly Emerged Adults*.** Freshly emerged adults for the experiment were obtained by placing 0.5 g of colored-psocid diet, five particles of cracked wheat, 20 mg wheat germ, and thirty 1-to 2-wk-old females in each of sixty 35-mm Petri dishes. The inner walls of the Petri dishes were coated with Fluon® to prevent psocids from escaping. The Petri dishes were then placed on perforated false floors in two plastic boxes (37 by 22 by 13 cm in height) which contained saturated NaCl solution beneath the false floors and were kept in an incubator maintained at 30 ± 1°C. After 7 d, all live psocids were removed from each Petri dish. The colored diet containing eggs in each 35-mm Petri dish was transferred to a 9-cm Petri dish containing 20 pieces of cracked wheat. Transfer was done in such a way that the top part of the colored diet in each 35-mm Petri dish remained at the top in a 9-cm Petri dish to ensure psocids could move freely after hatching. Sixty 9-cm Petri dishes were then placed in box (42 by 29 by 24 cm in height) containing saturated NaCl beneath the false floor to attain 75 ± 5% RH and held at 30 ± 1°C. *L. rufa* takes approximately 25 d to develop from egg to adult at 30°C (Gautam et al. 2010). Therefore, after 10 days, each Petri dish was checked daily for adult females. Freshly emerged adult females found were removed and used for determining reproductive parameters. The date each adult female was removed from a 9-cm Petri dish was noted. Adult females are easily distinguished from nymphs using body color - adults are brownish whereas nymphs are pale yellowish in color.

Diet Equilibration. Five pieces of cracked wheat were placed in each of one hundred and forty 35-mm Petri dishes, inner walls of which were coated with Fluon®. The contents of all Petri dishes were then equilibrated at room temperature and 75 ± 5% RH over a 4-wk period before use. Fifty grams of colored diet were also equilibrated under the aforementioned conditions. On the day daily checking of 9-cm Petri dishes for freshly emerged adult females was initiated, 20 mg of colored diet were added to each of the 35-mm Petri dishes. Freshly emerged females were transferred from 9-cm Petri dishes to 35-mm Petri dishes with equilibrated diet; each 35-mm Petri dish received a single female. A single freshly emerged male was also placed in each 35-mm Petri dish. The 20 mg of colored diet in each Petri dish provided a substrate for psocids to lay eggs. Petri dishes containing pairs of psocids were randomly assigned to each of seven plastic boxes (37 by 22 by 13 cm in height) containing saturated NaCl beneath the false floors.

Effects of Temperature on Reproductive Parameters. The seven plastic boxes, containing 35-mm Petri dishes with pairs of newly emerged adult male and female psocids and equilibrated diet, were randomly assigned to one of seven incubators set at temperatures of 25, 27.5, 30, 32.5, 35, 37.5, and 40°C. Because adult emergence in the 9-cm Petri dishes could not provide all the 140 adult females required to set up all the Petri dishes on a single day, care was taken to ensure that a similar number of freshly emerged adult females were allocated to each of the seven boxes (temperatures) each day until every box received 20 females. After each box received 20 females, all the adult males in the 9-cm Petri dishes were transferred to a single 9-cm Petri dish containing 15 g of red colored diet and 2.5 g of cracked wheat and were kept at 30 ± 1°C and 75 ± 5% RH. This was done to ensure that the males used for replacement of dead or lost males (paired with

females) during the course of the experiment were of similar age. However, loss or death of males seldom happened during the experiment.

Each Petri dish containing a pair of psocids was checked daily using a stereomicroscope (Stemi 2000-C, Carl Zeiss, Thornwood, NY) until the adult female in it died. During checking, any eggs found were counted and removed using a moist brush. When the amount of colored diet in a Petri dish was depleted to 30% of the original amount present (due to egg removal), 20 mg were added. However, addition of colored diet seldom happened. In order to keep the Petri dishes clean, psocid feces were removed using a moist brush during the checking of the Petri dishes for eggs. Boxes were also checked to ensure that the salt solution (NaCl) was still saturated; this was done by making sure that the desired amount of the solute and solution of the saturated solution were present in each box.

Data Analysis. The experiment had three temporal replications and the experimental design used was randomized complete block (RCBD) with sub sampling. All statistical procedures were accomplished using Statistical Analysis System software (SAS Institute 2001). PROC GLM was used for analysis of variance (ANOVA) to determine the effects of temperature on preoviposition period, postoviposition period, oviposition period, fecundity, longevity, and the percentage of total life span spent in oviposition. Data for the first five parameters and the percentage of the life span spent in oviposition were transformed using the square-root and arcsine square-root transformations, respectively, to stabilize variances before analysis. Untransformed means and standard errors are reported to simplify interpretation. Temperature-dependent equations for preoviposition period, postoviposition period, oviposition period,

oviposition rate, fecundity, longevity, and percentage of the life span spent in oviposition were developed by regressing data for each of these parameters against temperature using TableCurve 2D (Systat Software, Inc. 2002). Weekly survivorship data were subjected to survival analysis using PROC LIFEREG and the Wald chi-square to test the equality of the survival curves among different temperatures (SAS Institute 2002).

Life Table parameters. The net reproductive rate (R_o) for each temperature was calculated using age-specific life tables [$R_o = \sum l_x m_x$, where l_x and m_x are age-specific survival rate and fecundity, respectively] (Birch 1948). The generation time (T) for each temperature was calculated by adding development time from egg to adult (Gautam et al. 2010) to the preoviposition period. The intrinsic rate of increase (r) (Birch 1948) was calculated as:

$$r = \ln(R_o)/T.$$

The population doubling time, t, was calculated as:

$$t = 0.693/r.$$

Results

Temperature had significant effect on all the parameters studied. Fecundity increased with temperature up to 30°C and then declined (Table 1, Fig 3E). Numbers of eggs laid during a female's lifetime varied from 63 at 30°C to 28 at 40°C (Table 1). At 25, 27.5, 30, 35, and 37.5°C the highest oviposition rates (eggs/female/week) occurred in week 2, and oviposition rates attained were 8.2, 10.9, 13.7, 15.4, and 13.8 respectively (Fig. 1). At these temperatures, *L. rufa* laid 60, 64, 71, 89, and 94%, respectively, of the total number of eggs in the first four weeks. At 32.5°C, the highest oviposition rate occurred in week 1 (14.7) and 88% of all eggs were laid in the first four weeks. At 40°C

the highest oviposition rate occurred in week 1 and was 8.7 (Fig. 1); *L. rufa* laid 94% of all eggs in the first four weeks at this temperature. The steepness of the decline in oviposition rate from the peak rate increased with temperature until 37.5°C then declined (Fig. 1). Highest individual oviposition rate recorded was at 35°C, and was 3.1 eggs per day (21.8 eggs per wk); the oviposition period for this female was 34 days, during which it laid 106 eggs. However, the highest individual fecundity was recorded at 32.5°C (137 eggs). Mean weekly oviposition rate increased with temperature up to 35°C (4.7 eggs/female/wk) and then declined (Fig. 2, Table 2).

Survival analysis of the weekly survivorship data showed significant differences among insects exposed to different temperatures (Wald $\chi^2 = 775.9$; df = 1; $P < 0.0001$). Survivorship decreased more rapidly with increasing temperature. At 25, 27.5, 30, 32.5, 35, 37.5, and 40°C, it took 32, 32, 22, 15, 17, 12, and 9 wks, respectively, for all females to die (Fig. 1). For higher temperatures (32.5, 35, 37.5 and 40°C), the steepest decline in survivorship occurred immediately or nearly so after the peak oviposition rate had been reached (Fig. 1).

Preoviposition and postoviposition periods generally decreased with temperature then increased (Fig. 3A & B, Tables 1 and 2). The longest mean preoviposition period (2.53 d) was recorded at 25°C, which decreased with temperature until 35°C and increased (Fig 3 A, Table 1). The longest mean postoviposition period (42.9 d) was recorded at 25°C, it decreased to 6.2 d at 37.5°C before increasing to 8.2 d at 40°C (Fig. 3B, Table 1).

Oviposition period and longevity also decreased with temperature (Fig. 3C & D, respectively; Tables 1 and 2). At 25°C, these parameters averaged 93 and 139 d,

respectively, and at 40°C, they were 26 and 36 d, respectively. The longest lifespan recorded was 219 d at 27.5°C. The percentage of the total lifespan spent in oviposition increased from 67% at 25°C to 82% at 32.5°C and then declined to 74% at 40°C (Fig 3 F, Tables 1 & 2).

Generation time and population doubling time declined with temperature until 32.5°C (22.8 and 3.9 d, respectively) and then increased (Table 3). Intrinsic rate of population increase increased with temperature until 32.5°C (0.18) and then declined (Table 3). The net reproductive rate increased with temperature until 32.5°C (60.24) and then declined at higher temperatures (Table 3).

Discussion

All reproductive parameters varied with temperature. Intrinsic rate of population increase for *L. rufa* increased with temperature until 32.5°C (0.179) and then declined. If the intrinsic rate of increase at 32.5°C is considered the optimal fitness of 1, then the fitness of *L. rufa* at 25, 27.5, 30, 35, 37.5, and 40°C equals 0.53, 0.72, 0.90, 0.86, 0.84, and 0.72, respectively. Highest intrinsic rates of increase for *Lepinotus reticulatus* (Opit et al. 2010a), *Liposcelis badia* Wang, Wang, and Lienhard (Jiang et al. 2008), *L. bostrychophila* (Wang et al. 2000), *L. decolor* (Tang et al. 2008), *L. paeta* (Wang et al. 2009), and *L. tricolor* Badonnel (Dong et al. 2007) occurred at 32.5, 27.5, 30, 32.5, 32.5, and 30°C, respectively. Intrinsic rates of increase at these temperatures were 0.128, 0.0455, 0.0946, 0.0609, 0.0542, and 0.0367, respectively. At optimal temperatures for intrinsic rate of increase, *L. rufa* has the highest potential for population growth among these psocid species. Even at suboptimal temperatures for intrinsic rate of population

increase, the potential for *L. rufa* population growth appears to be higher than that of other *Liposcelis* spp.

Fecundity was highest at 30°C (63 eggs per female). The lowest fecundity was observed at 40°C (28 eggs per female), which may indicate this species is adapted to live in high temperature environments. I found that *L. rufa* can live for up to 9 wk at 40°C. The optimum temperatures for population growth of most psocid species infesting stored products seems to range from 30 to 35°C (Rees and Walker 1990). However, Gautam et al. (2010), in their study on the effects of temperature and relative humidity on *L. rufa* population growth and development, demonstrated this species can reproduce at temperatures as high as 40°C. They found that populations of *L. rufa* increased under conditions of 22.5 to 30°C at 55% RH and 22.5 to 40°C at 75% RH; and population growth at 32.5 and 37.5°C was similar. However, a temperature of 40°C resulted in retarded population growth which may partly be explained by the fact that only 34% of eggs that hatch develop into adults at 40°C (Gautam et al. 2010). The observation that the highest population growth for *L. rufa* occurs at 35°C (Gautam et al. 2010) and the fact that the highest oviposition rate is at 35°C, a temperature at which *L. reticulatus*, *L. brunnea,* and *L. pearmani* would barely grow (Opit and Throne 2008, 2009; Opit et al. 2010a, 2010b) seem to suggest that *L. rufa* is suited to warm and humid environments. This may explain why *L. rufa* infestation has been found on stored wheat in Oklahoma but not in Kansas.

L. decolor and *L. paeta* are the only other psocid species believed to be adapted to higher temperatures (Beckett and Mortan 2003). In the present study, I found that the intrinsic rate of increase, fecundity, and longevity of *L. rufa* are greater than those of *L.*

decolor and *L. paeta* at higher temperatures (Tang et al. 2008, Wang et al. 2009). For example, at 37.5°C, intrinsic rate of population increase, fecundity, and longevity for *L. decolor* and *L. paeta* are 0.0112 and 0.0504; 20.3 and 17.8; and 27 and 25 d respectively, whereas the values of these parameters for *L. rufa* are 0.151, 44.4, and 38 d, respectively. This may mean that *L. rufa* is more suited to warm climates than *L. paeta* and *L. decolor*. According to Guedes et al (2008), the presence of heat inducible proteins in genus *Liposcelis* may explain the tolerance of these three species to higher temperatures.

As expected, oviposition period was longer and the percentage of eggs laid in the first 4 wk was smaller at lower temperatures than at higher temperatures. At 25, 27.5, 30, 35, and 37.5°C, oviposition peaked in the second week and oviposition rates (eggs/female/week) were 8.2, 10.9, 13.7, 15.4, and 13.8, respectively. The last egg oviposited was after 31, 25, 21, 17, and 10 wk, respectively, and the percentages of eggs laid in the first 4-wk were 60, 64, 71, 89, and 94%, respectively. For 32.5°C, oviposition rate was highest in week 1 (14.7) and the last egg oviposited was after 13 wk; *L. rufa* laid 88% of the total number of eggs in the first four weeks. At 40°C, oviposition peaked in the first wk, oviposition rate was 8.7; and the last egg oviposited was after 7 wk. At this temperature, 94%, of the eggs were laid in the first 4 wk. These observations may be explained by the fact that the physiological processes of converting resources to eggs and of egg maturation are temperature dependent (Berger et al. 2008). According to them, under certain thermal regimes, realized fecundity can be limited by the temperature dependence of egg maturation and oviposition, because at suboptimal temperatures, insect would be diverting the energy towards the maintenance of body functions. Other studies have also determined that oviposition peaks occur earlier with increasing

temperature. For example, *L. reticulatus* oviposition which peaked in week 3 at 25°C peaked at week 2 at 32.5° (Opit et al. 2010a). *L. rufa* produces the largest number of eggs at 30°C; *L. bostrychophila* at 27.5 and 30°C (Wang et al. 2000); *L. reticulatus* (Opit et al. 2010a), *L. tricolor* (Dong et al. 2007), and *L. paeta* (Wang et al. 2009) at 27.5°C, and *L. decolor* (Tang et al. 2008) at 32.5°C. At these optimal temperatures, *L. rufa, L. bostrychophila, L. reticulatus, L. tricolor, L. paeta,* and *L. decolor* produce 63, 75, 41, 54, 108, and 130 eggs, respectively. *L. rufa* produces 44 and 28 eggs at 37.5 and 40°C, respectively. As already mentioned, other species which have been documented to oviposit large numbers of eggs at high temperatures are, *L. decolor* (Tang et al. 2008) and *L. paeta* (Wang et al. 2009), which produce 74 and 25, and 102 and 20 eggs, respectively, at 35 and 37.5°C. It is quite remarkable for these small (up to 1mm long), soft bodied insects to produce such a large number of eggs at these high temperatures and indicates an adaptation to warmer climates as mentioned earlier. *L. badia* produces an average of 19, 30, 18, and 15 eggs at 27.5, 30, 32.5, and 35°C, respectively, but produces the largest number of eggs (52) at 20°C (Jiang et al. 2008). Therefore, based on fecundity alone, the order of increasing adaptation to warm climates for these psocids is *L. badia, L. reticulatus, L. tricolor, L. bostrychophila, L. decolor, L. paeta,* and *L. rufa*. At the optimal egg laying temperatures, the average lifetime fecundities of *L. bostrychophila, L. paeta,* and *L. decolor* are higher than those of *L. badia, L. reticulatus, L. rufa,* and *L. tricolor*; coupled with this, the first group can lay on average 52, 50, and 65 eggs, respectively, at the low temperature of 20°C. These two facts may explain why *L. bostrychophila, L. decolor,* and *L. paeta* are much more serious pests of stored products worldwide compared to *L. badia, L. reticulatus, L. rufa,* and *L. tricolor*. In addition, the

fecundity of *L. entomophila* is probably higher than that of *L. reticulatus* based on a study by Opit and Throne (2008a) which showed that the maximum number of progeny produced by five *L. reticulatus* females in 32 d at 30°C on a diet of cracked wheat was 115, while *L. entomophila* produced 502. I found some *L. rufa* individuals that were capable of prolific egg production, laying up to 7 eggs at 32.5 and 35°C in one day. A psocid egg measures 0.33 to 0.38 mm in length (Kučerová 2002b), this fact, together with the small size of psocid (1mm) implies that *L. rufa* can lay about 250% of the total body volume of eggs per day.

L. rufa and other aforementioned psocid species produce fewer eggs compared to stored-product beetle pests. For example, *Rhyzopertha dominica* (Fabricius) (Coleoptera: Bostrichidae) and *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) produce 400 eggs in a lifetime of 3 mo; *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) produces up to 1,000 eggs in a lifetime of a few months (Pedersen 1992, Rees 2004). According to Throne (1994) a maize weevil female, *Sitophilus zeamais* Motschulsky, can lay as many as 6.7 eggs per day at optimal conditions. However, psocids appear to compensate for their low fecundity by having higher intrinsic rates of increase. For example, the intrinsic rate of increase of *L. rufa* at 25°C is 0.097 while that of *T. castaneum* ranges between 0.005 and 0.025 (Pimentel et al. 2006). This may explain why much larger psocid populations are found infesting stored products compared to beetles.

I observed that *L. rufa* oviposition period and longevity declined with increasing temperature. A possible explanation for this may be that the higher egg maturation rates that occur at higher temperatures are associated with an overall higher metabolism which could reduce the life span (Papaj 2000, Jervis et al. 2005). At higher temperatures, they

may also be allocating significantly more energy resources to egg production than maintenance of body functions thereby resulting in reduced performance and survival (Papaj 2000, Carey 2001, Jervis et al. 2005, 2007). It is reasonable that at 25 and 40°C, *L. rufa* has a proportionately shorter oviposition period than at optimal temperatures because of the diversion of resources from egg production and maturation that may occur at these temperatures. This may also explain why the percentage of the total lifespan spent in oviposition increased from 67% at 25°C to 82.0% at 32.5°C and then declined to 74% at 40°C. Decline in oviposition period with temperature has also been shown in *L. reticulatus* (Opit et al. 2010a), where this parameter increased from 79% at 22.5°C to 85% at 32.5°C and declined to 75% at 35°C. Similar results have been demonstrated for *L. badia* (Jiang et al. 2008), *L. decolor* (Tang et al. 2008), and *L. paeta* (Wang et al. 2009). Moreover, longevity has also been shown to decline with increasing temperature in *L. badia*, *L. reticulatus*, *L. tricolor*, *L. decolor*, and *L. paeta*. However, contrary to what has been observed for other psocid species, longevity of *L. bostrychophila* increased with increasing temperature from 20°C until 30°C and then declined (Wang et al. 2000). Average life span of *L. rufa* at 25°C (139 d) is higher when compared to *L. badia*, *L. bostrychophila, L. reticulatus*, *L. decolor*, *L. paeta*, (60, 85, 39, 71 and 107 d, respectively). However, longevity of *L. tricolor* is exceptionally longer (262 d at 20°C), compared to other psocids.

Preoviposition period at 25, 27.5, 37.5, and 40°C was longer than at of 30, 32.5, and 35°C, it declined with temperature up to optimum temperature range and then increased. This is most probably due to already stated reasons related to resource allocation, egg production, and egg maturation. Similar trends were demonstrated for

preoviposition period in *L. badia*, *L. bostrychophila*, *L. decolor*, and *L. tricolor*. However, Opit et al. (2010) only observed a decline in preoviposition period of *L. reticulatus* with increasing temperature. Postoviposition period declined with increasing temperature up to 37.5°C and then increased for the same reasons. Similar trends were shown by Opit et al. (2010). However, they found that all *L. reticulatus* adults died within 8 and 4 d after cessation of oviposition at 25 and 27.5°C. In the case of *L. rufa*, I found this period to be 43 and 27 d, respectively.

My research has shown that *L. rufa* has a higher intrinsic rate of increase compared to other psocid species. It oviposits over a wide temperature range of 25 to 40°C, but the greatest numbers of eggs are laid at 30°C. *L. rufa* appears to be adapted to surviving in higher temperatures and relative humidities (40°C and 75% RH) and may therefore be a problem in hot and humid climates. I have also shown that *L. rufa* adults can live for 7 months at temperatures of 25 and 27.5°C. Finally, I have developed temperature-dependent equations for preoviposition period, postoviposition period, oviposition period, fecundity, longevity, oviposition rate, and percentage of lifespan spent in oviposition, which can be used in simulation models to aid in developing more effective management strategies for this species.

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Footnotes

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Table 1. Effects of constant temperatures on *Liposcelis rufa* preoviposition period (mean ± SE), oviposition period, postoviposition period, longevity, fecundity, and the percentage of adult lifespan spent in oviposition.

Temp (°C)	Preoviposition period (d)	Oviposition period (d)	Postoviposition period (d)	Longevity (d)	Fecundity (eggs/♀)	% of life spent in oviposition
25	2.53 ± 0.55	93.3 ± 4.6	42.9 ± 2.7	138.7 ± 2.1	44.7 ± 5.9	67.4 ± 2.9
27.5	1.51 ± 0.19	90.6 ± 1.5	27.1 ± 3.3	119.1 ± 4.8	54.6 ± 3.8	78.6 ± 1.7
30	0.99 ± 0.29	66.6 ± 2.6	19.8 ± 1.5	87.3 ± 4.1	62.5 ± 4.7	78.3 ± 1.1
32.5	1.14 ± 0.33	45.2 ±0 .5	9.4 ± 0.6	55.7 ± 0.2	58.6 ± 5.6	81.9 ± 1.1
35	0.85 ± 0.37	40.9 ± 3.9	10.2 ± 0.5	52.1 ± 3.9	54.1 ± 4.8	78.7 ± 1.3
37.5	2.13 ± 1.14	29.8 ± 2.4	6.2 ± 0.8	38.2± 1.4	44.4 ± 9.1	78.9 ± 5.2
40	1.99 ± 0.93	26.3 ± 2.7	8.2 ± 1.1	36.4 ± 1.8	27.9 ± 5.7	73.9 ± 5.1

F values of ANOVA results for the preoviposition period, oviposition period, postoviposition period, longevity, fecundity, and percentage of lifespan spent in oviposition were 14.32, 17.14, 6.51, 25.94, 7.31, and 1.69. In all cases df = 6,12 and $P < 0.0001$.

Table 2. Parameters (± SE) describing the effects of constant temperatures on *Liposcelis rufa* preoviposition period, oviposition period, postoviposition period, oviposition rate, longevity, fecundity, and % of life spent in oviposition.

Subject	Maximum R^2	R^2	*F*	a	b	c
Preoviposition period	0.26	0.03	1.9	7.65 ± 3.20	-0.011 ± 0.006	0.000005 ± 0.000003
Oviposition period	0.96	0.92	123.8	209.75 ± 20.52	-0.217 ± 0.039	0.00006 ± 0.00001
Postoviposition period*	0.94	0.92	116.7	-410.33 ± 76.29	-5.54 ± 1.192	7861.068 ± 1195.954
Oviposition rate	0.63	0.48	11.4	-8.169 ± 3.063	0.0203 ± 0.006	-0.0000079 ± 0.000001
Longevity	0.98	0.96	261.5	342.73 ± 20.87	-0.40 ± 0.039	0.00013±0.000017
Fecundity*	0.53	0.43	9.8	945.421± 228.65	-14.46 ± 3.57	-13499.01± 3584.39
% life spent in Oviposition*	0.39	0.24	4.9	434.286 ± 125.12	-5.40±1.95	-5766.537± 1961

In the case with an asterisk (*), equation is of the type $y = a + bx + c/x$ with an adjusted R^2 value. In all other cases, equation is of the type $y = a + bx^2 + cx^4$. P values and lack-of-fit *P*-values for preoviposition period, oviposition period, postoviposition period, oviposition rate, longevity, fecundity and percentage of life span spent in oviposition were 0.82, 0.056, 0.59, 0.59, 0.08,

0.99, and 0.89, respectively and $P = 0.17$, $P = 0$, $P = 0$, $P = 0.0006$, $P = 0$, $P = 0.0013$, and $P = 0.0196$, respectively. In all cases df = 2,20.

Table 3. Life table parameters (mean ± SE) of *Liposcelis rufa*.

Temperature (°C)	*N*	*r*	R_o	*T*	*t*
25.0	38	0.094 ± 0.004	43.5 ± 6.71	39.8	7.4
27.5	53	0.128 ± 0.002	52.7 ± 3.24	31.0	5.4
30.0	57	0.161 ± 0.003	59.75 ± 5.47	25.4	4.3
32.5	50	0.179 ± 0.005	60.24 ± 7.82	22.8	3.9
35.0	59	0.154 ± 0.004	51.35 ± 6.07	25.5	4.5
37.5	53	0.151± 0.007	37.65± 6.24	23.7	4.6
40.0	55	0.129± 0.013	24.65± 7.28	24.0	5.5

N, number of females in the analysis; *r*, intrinsic rate of population increase; R_o, net reproductive rate; *T*, generation time (d); and *t*, population doubling time (d).

Figure Captions

Fig. 1. Oviposition and survival of *Liposcelis rufa* at constant temperatures.

Fig. 2. Mean weekly oviposition rate of *Liposcelis rufa* at constant temperatures. Parameters for the fitted line are in Table 2.

Fig. 3. Preoviposition period, postoviposition period, oviposition period, longevity, fecundity, and percentage of life spent in oviposition of *Liposcelis rufa* at constant temperatures. Parameters for the fitted lines are in Table 2.

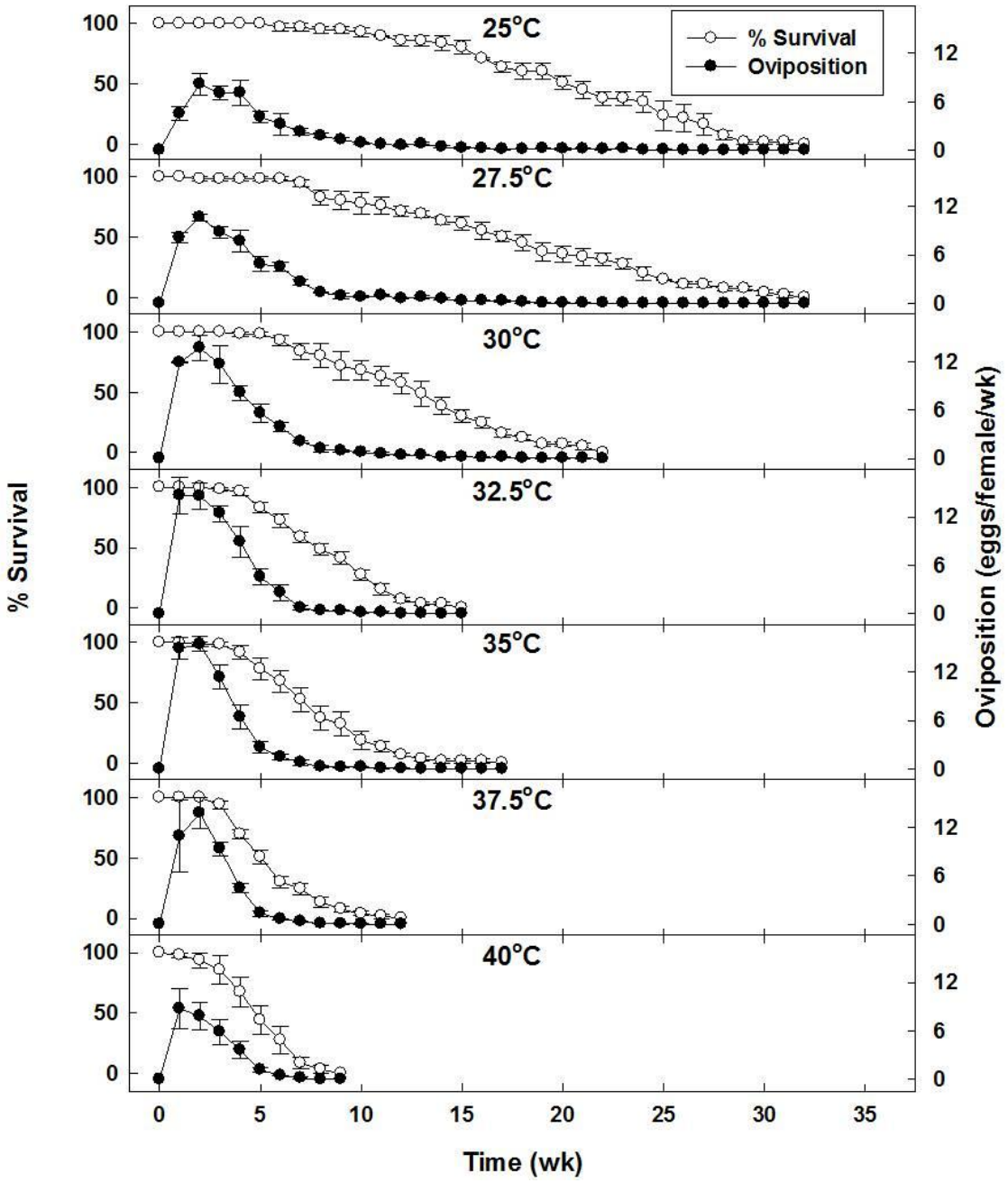
25°C
27.5°C
30°C
32.5°C
35°C
37.5°C
40°C
% Survival
Oviposition
% Survival
Oviposition (eggs/female/wk)
Time (wk)
0
5
10
15
20
25
30
35
0
50
100
0
6
12

Fig. 1

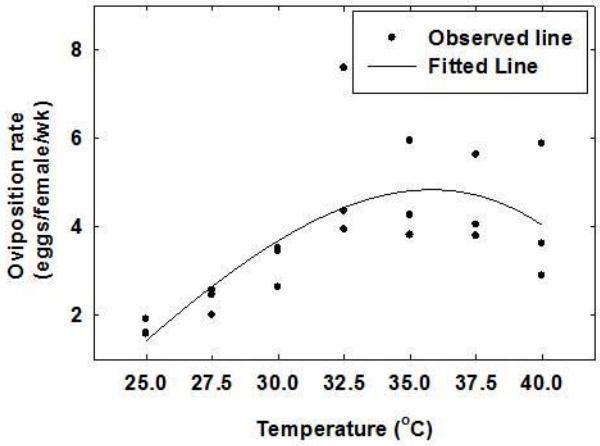
Observed line
Fitted Line
Oviposition rate
(eggs/female/wk)
8
6
4
2
25.0
27.5
30.0
32.5
35.0
37.5
40.0
Temperature (°C)

Fig. 2

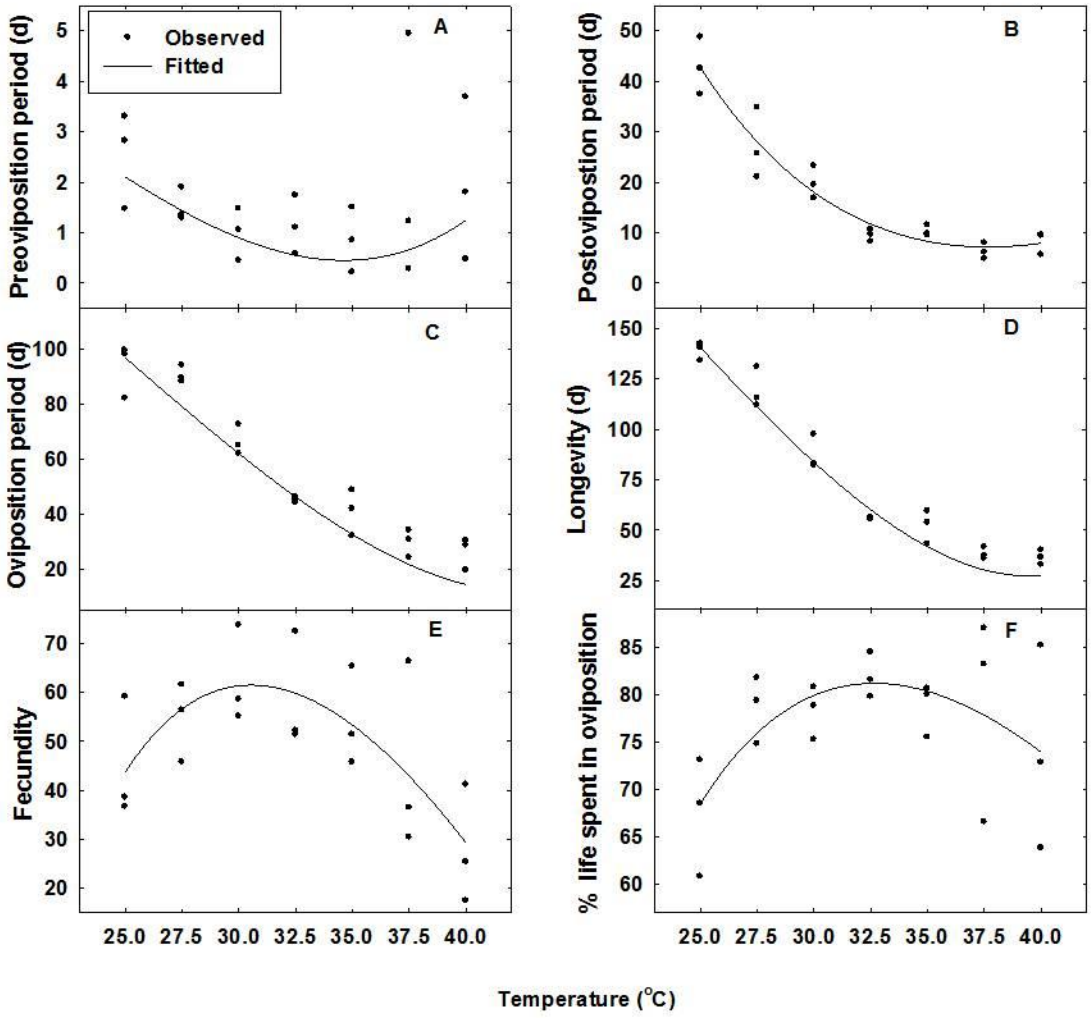
Observed
Fitted
A
B
C
D
E
F
Preoviposition period (d)
Postovipostion period (d)
Oviposition period (d)
Longevity (d)
Fecundity
% life spent in oviposition
25.0 27.5 30.0 32.5 35.0 37.5 40.0
Temperature (°C)

Fig. 3.

CHAPTER V

CONCLUSIONS

In the last two decades, psocids have become recognized pests of stored products all over the world, including the United States. Despite this, very little information is available on their ecology and biology. However, a good understanding of pest ecology is crucial to the development of effective management strategies. Given the lack of information on *L. rufa*, I initiated experiments to study *L. rufa* biology and the ecology. I investigated the effects of eight constant temperatures (22.5, 25, 27.5, 30, 32.5, 35, 37.5 and 40°C) and four relative humidities (43, 55, 63, and 75%) on the population growth, effects of eight constant temperatures and 75% RH on development, and effects of seven temperatures and 75% RH on reproductive parameters of the psocid *Liposcelis rufa*.

The study on population growth at different temperatures and relative humidities showed that *L. rufa* can survive and multiply at a low relative humidity of 55% RH at 22.5 to 30°C and at the high temperature of 40°C at 75% RH. The optimal conditions for reproduction for this species are 35.0°C and 75% RH; under these conditions *L. rufa* population increased by up to 73-fold. The optimal temperature range for population growth of L. rufa is 30-37.5°C. The ability of *L. rufa* to reproduce at 55% RH (at temperatures 22.5 to 30°C) and their ability to rapidly multiply at higher temperatures

(37.5 and 40°C) and high relative humidity (75%) implies that this species may have a broader ecological distribution compared to other psocid species. The lower and upper developmental thresholds for *L. rufa* were calculated to be 8.5 and 38.7°C, respectively, which aids to the earlier statement of adoption of this species to ecological areas with varying temperature and relative humidity.

My findings from the study where I investigated the effects of temperature on *L. rufa* development show that *L. rufa* males have a shorter developmental period from egg to adult compared to females. This might be due to the fact that females usually have one more instar compared to males - *L. rufa* males have two to four instars whereas females have two to five instars. The percentage of males with two, three and four instars were, 31, 54, and 14 %, respectively whereas the percentage of females with two, three, four, and five instars were 2, 24, 42, and 12%, respectively. The shortest development period occurred at 37.5°C; at this temperature, development was completed in 17.5 d for males and 21.6 d for females. Temperature had a significant effect on the developmental time for all life stages of *L. rufa*. However, egg viability was not affected by temperature. We found nymphal survivorship to be extremely low at 40°C. This low nymphal survivorship at 40°C means high temperature is detrimental to psocid development. I have developed temperature dependent equations which can be used to predict developmental periods for male and female *L. rufa*. In the study where I investigated the effects of temperature on the reproductive parameters of *L. rufa*, my data show that *L. rufa* has a higher intrinsic rate of population increase (0.18) and a shorter population doubling time (3.9 d) compared to other *Liposcelis* species. It oviposits at a wider range of temperatures ranging from 25 to 40°C; and the highest fecundity was at 30°C (63 eggs). *L. rufa* can

survive for up to 9 wk at 40°C and up to 32 wk at 25 and 27.5°C. I have also developed temperature-dependent equations which can be used to predict reproductive parameters of *L. rufa*.

Given that *L. rufa* has a short life cycle, high intrinsic rate of increase, and an ability to multiply rapidly at high temperatures over a range of relative humidities, it can be expected to be a serious stored product pest in Oklahoma. Winter wheat production contributed $1.082 billion to the Oklahoma economy in 2008 (NASS 2009). Following harvest in June, wheat is stored before selling. According to NASS and Oklahoma Agricultural Statistics Service data states, 89% of the total stored wheat is stored commercially whereas 11% is stored on farm. Farmers are negative feed-back traders since they sell after the price increases and tend to hold when the price declines. Therefore, depending on market value, wheat can be stored for longer periods making it more susceptible to increased infestation by pests such as psocids.

Wheat stored on-farm is especially more vulnerable to infestation by psocids and other stored-product insects primarily due to limitations of infrastructures that can be used towards preventing invasions and to control population explosions. However, simple techniques such as sanitation, storage of low moisture content wheat, sealing leaks in storage structures, and close monitoring of storage conditions will prevent population explosions. My results have demonstrated *L. rufa* population will grow quickly in hot and humid environments, but are inhibited by low relative humidities (< 55%), especially at higher temperatures. Broken kernels and grain spills in storage areas, cracks, and crevices where relative humidity is higher than ambient provide ideal environments for psocid multiplication. Physical management approaches that minimize psocid infestations of

storage structures include proper sanitation of storage areas and equipment prior to harvest and bin sealing, cleaning, and disinfestation using either heat or pesticides. Given that high moisture in grain can encourage fungal growth and causes increase in relative humidity of the storage environment, storing well dried wheat (<13% moisture content) is important for the prevention of psocid infestation. Cooling stored grain using aeration also helps to slow the growth of psocid populations.

My research is the first ecological study conducted on *L. rufa* and has contributed valuable information that improves our understanding of *L. rufa* ecology. Information from my research can be used to elucidate *L. rufa* population dynamics and to facilitate the development of effective management strategies against food-associated psocids.

VITA

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Candidate for the Degree of

Master of Science

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Biographical:

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Name: Sandipa G. Gautam Date of Degree: December, 2010

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: ECOLOGICAL STUDIES OF THE PSOCID *LIPOSCELIS RUFA* BROADHEAD (PSOCOPTERA: LIPOSCELIDIDAE)

Pages in Study: 104 Candidate for the Degree of Master of Science

Major Field: Entomology

Scope and Method of Study:

Psocids (Psocoptera) have risen to prominence as serious pests of stored-products worldwide in the last two decades. However, very little is known about their ecology and biology which is crucial for the development of effective management strategies. In this study, I investigated the effects of constant temperatures and relative humidities on the population growth, effect of constant temperatures at optimal relative humidity on the development and reproductive parameters of *Liposcelis rufa* in order to elucidate the influence of environmental conditions on its biology and the ecology.

Findings and Conclusions:

My research has shown that *L. rufa* can survive and multiply at a low relative humidity of 55% at temperatures of 22.5 to 30°C and a high temperature of 40.0°C at 75% RH. The optimal conditions for reproduction for this species are 35.0°C and 75% RH where population increased 73- fold. The shortest developmental time from egg to adult was recorded at 37.5°C; at this temperature development of female was completed in 21.6 d. Males have shorter life cycle than females and this may be due to the fact that females have one more instar compared to males. *L. rufa* males had two to four instars whereas females had two to five instars. Temperature has significant effect on development time for all developmental stages. Also, my work has demonstrated that *L. rufa* has a higher intrinsic rate of population increase compared to other psocid species (0.18). It oviposits at a wider range of temperature from 25 to 40°C, and the highest fecundity was recorded at 30°C (63 eggs).The highest oviposition rate was recorded at 35°C (15.4 eggs/ female/ wk), 2 wk after the initiation of oviposition. *L. rufa* can live up to 9 wk at 40°C, and the longest living individual lived 219 d at 27.5°C. Given its ability to multiply rapidly at high temperatures and relative humidities, its short life cycle, high intrinsic rate of increase, and the ability to live for long, especially at higher temperatures suggests *L. rufa* has great potential to be a serious stored product pest in hot and humid climates. In addition, it is likely to have a broader ecological distribution because it can survive and multiply at temperatures of 22.5 - 40°C and 55-75% RH. Finally, the temperature-dependent equations I have developed for *L. rufa* developmental stages and reproductive parameters can be used to elucidate its population dynamics and to facilitate the development of effective management strategies for this pest.

ADVISER'S APPROVAL: Dr. George P. Opit